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# STUDIES IN THE ECOLOGY OF BRITISH GRASSHOPPERS

By E. J. Clark.

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(Read 19th November, 1947.)
With 1 Text-figure.

## Preface

BY DR. B. P. UVAROV, C.M.G., F.R.E.S.

The author of the present paper was not an entomologist and he undertook this work as a relaxation from strenuous studies and research in a different field (physiology and biochemistry), but his approach to grasshopper ecology was anything but amateurish. In my much too brief association with Clark, I was deeply impressed by his exceptional clarity of thinking which enabled him to envisage the problem as a whole and, at the same time, to appreciate its many special aspects. In undertaking the investigations, Clark aimed at presenting detailed accounts of the autecology of British species of Acrididae, in relation to their general distribution and ecological characteristics elsewhere. He then hoped to present a classification of British habitats, analysed from the point of view of their suitability for each species of grasshopper. His plans extended also to a detailed study of the ecological and geographical distribution of genotypic colour and pattern variations in local populations. A piece of work, preliminary to these latter investigations, was his attempt to evolve a rational standard nomenclature of colour and pattern variations (Clark, 1943, *Ent. mon. Mag.* **79 : 91**). All these plans came to an abrupt end through Clark's sudden death, after a brief illness, at the age of 24 (Carpenter, 1945, *Ent. mon. Mag.* **81 : 143**).

Fortunately, a few weeks before his death, Clark decided to write up his main results, in order to clarify some of his ideas, and several chapters were completed, or nearly so. When asked by Professor G. Hale Carpenter to look through manuscripts and notes left by Clark, I tried to save from oblivion all that appeared to me of lasting value. Many of his notes and uncompleted sections had to be left unpublished, and they are preserved in the Hope Department, University Museum, Oxford.

The chapters which are now being published may appear insufficiently finished, but they contain many original ideas and suggestions which should provide a stimulus and inspiration to future workers on grasshopper ecology, a subject which Clark certainly succeeded in presenting as a most fascinating field of research.

## Introduction.

There has been little detailed work on the ecology of British Acrididae, that of Diver and Diver (1933) being the only notable exception.

The main reason for this is perhaps the limited size of the British fauna, which comprises nine species, only eight being at all generally distributed. Such a small group of species, all of the subfamily ACRIDINAE, and of very similar life-history and habits, has, however, advantages as a subject for ecological work, since the homogeneity of the group permits specialisation of methods of observation and experiment to a fuller degree, than with a large and varied fauna.

The data recorded below are a result of four years' (1941–1944) irregular observations, mostly in Surrey (North Downs area), Berkshire, and Oxfordshire (Oxford district), with some records from Buckinghamshire, Gloucestershire and Monmouthshire. Within this area as wide a range of grasshopper habitats as possible has been surveyed, using a standard routine of recording the characters of vegetation, soil and topography of each habitat, and of determining abundance of all grasshoppers and of individual species.

The species dealt with are the following :—

*Stenobothus lineatus* (Panzer), *Omocestus viridulus* (L.), *Omocestus ventralis* (Zetterstedt), *Myrmeleotettix maculatus* (Thunberg), *Chorthippus bicolor* (Charpentier), *Chorthippus albomarginatus* (de Geer) and *Gomphocerippus rufus* (L.).

## APPROACH TO THE PROBLEM.

This is not the place for an exhaustive survey of work on the ecology of ACRIDIDAE, but it is worth while to consider briefly the theoretical aspects of the subject as a whole, and its relation to the ecology of other groups of animals.

The systematic and biogeographical work on ACRIDIDAE was an essential preliminary to the more recent and detailed investigations of the ecology of ACRIDIDAE. It was in systematic description of faunas that details of life-history and habitat preferences were first recorded, and though early examples of this provide only very scanty and irregular information, a few contain ecological observations of some value (*e.g.*, Zacher, 1917 ; Fruhstorfer, 1921). The systematic accounts of the British fauna give quite inadequate and often misleading ecological information (Lucas, 1920 ; Burr, 1936).

The biogeographical work of Morse (1904, 1907) is generally held to have begun the study of the ecology of ACRIDIDAE ; he described preferences of N. American ACRIDIDAE for particular local environmental conditions, relating them to their gross geographical distribution. Vestal (1913) made the first observations on the relation of grasshoppers to local environmental conditions, and drew some important general conclusions. He analysed the specificity of each species to a given range of habitat conditions in terms of the way in which these habitats satisfy the climatic, feeding, or reproductive requirements of the species, and pointed out, in particular, how variations of vegetation structure and composition modify local habitat conditions in these respects ; he recognised how in a given habitat the limiting conditions for occurence of more than one species may commonly be satisfied, and described associations of grasshoppers characteristic of particular types

of habitat (which he characterised mainly by their vegetation). Another important point was the more limited range of conditions suitable for reproduction and for nymph activity than for adult activity, so that constancy of occurrence in the more limited range was higher than for habitats occupied mainly by more or less erratic spread of adults—a separation of the concept of abundance in a habitat from that of constancy or frequency in that type of habitat in general. This work was also done in N. America, and in the period of early development of the ideas of community ecology associated particularly with the names of Clements and Shelford ; Shelford, indeed (1912, 1913), was at the same time advancing similar theoretical considerations from work on other groups of animals, notably CICINDELIDAE. While Vestal's theoretical discussion is thorough and well balanced, there is a tendency to over-emphasise specific composition rather than structure of the vegetation of the habitat. This tendency is symptomatic of the desire to recognise associations of animals and plants as synecological units or biocoenoses, which characterises the American school particularly, but which has also more recently spread to Europe. The danger that this involves is the multiplication of descriptions of individual biocoenoses for their own sake, without investigation of the processes involved in their maintenance or transmutations. The interpretation of dynamic equilibria in communities of plants and animals involves to some extent specific relations between individual species of associated animals or plants (food, host-parasite relations, etc.), but, often to a much greater extent, the relations determined by mechanical or climatic factors. The emphasis on specificity of membership of a biocoenosis has led to an uncritical attitude, for instance, in the description of species of plants as "indicators" of conditions favourable for animal species ; where the interrelations really are specific, as with the host-parasite or food relations, then indicators may be absolute, but more often the interrelations depend on a common relation to microclimatic conditions and indicators are of limited validity. The indicator concept, developed by Clements, an outcome of work on vegetation, has its value in plant and animal ecology, provided its underlying principles, and consequent limitations, are recognised. Vestal did, indeed, avoid a danger of the Clements-Shelford school of thought, that of relating ecological history of animal communities to the more or less hypothetical successional changes of the vegetation communities associated with them. Changes of vegetation must necessarily have important effects on animals whose mode of life is closely related to vegetation as is that of grasshoppers, but Vestal rightly pointed out that ecology of such animals must primarily be considered in relation to the factors directly limiting and controlling their occurrence, and that any relation to such environmental phenomena as seral changes of the vegetation must be interpreted in terms of these primary factors.

Two main points may be made so far from this discussion. First, grasshoppers, like other groups of animals, depend for their occurrence on climatic conditions, general and local, on food supply, on suitable sites for reproductive activity, and on relations with other animals,

particularly predators, parasites, and other occupants of the same ecological niche (potential competitors); opinions about the relative importance of these factors vary according to theoretical interpretations and to type of experimental observation. Second, simple descriptions of the associations in which grasshoppers may take part are valuable in preliminary surveys of material for ecological analysis, but are of little further value unless interpreted in terms of the fundamental factors determining occurrence together of the various grasshoppers, and determining their interaction with each other and with all other features of the habitat; in short, knowledge of autecology of all members of a biocoenosis is a necessary condition for full understanding of its synecology.

The most prevalent and fruitful view of the relation of Acrididae to their environment is that which emphasises the importance of climatic conditions, and especially of microclimates due to variations of topography or vegetation structure; for animals with such a comparatively wide range of palatable food plants, and with such a limited range of normal movement over the vegetation cover, local variations of microclimate are of great importance. The value of this point of view has been emphasised by Uvarov (1928, 1932, 1933). The crucial features of local climate are of course temperature and humidity, and Franz (1930) has shown how the behaviour of the layer of air near the earth's surface which mainly determines these features is modified very significantly by the local variations of vegetation or topography which are related to occurrence of a variety of Orthoptera and Coleoptera. A number of investigators on the local distribution of grasshoppers in relation to plant associations have interpreted results in terms of distribution of microclimatic conditions, but of those who have attempted to make direct determinations of temperature and humidity in the relevant habitats (*e.g.*, Gause, 1932; Buistritski, 1933; Strohecker, 1937), none has paid great attention to local variations of these conditions within a habitat, only gross, overall determinations being used; also there is little detailed work on differential distribution within a grossly uniform plant association, except that of Rubtzov (1932*a*), perhaps because of the difficulties in the way of an accurate method of observing and recording such detailed variation of abundance. It is still, however, held by some workers (*e.g.*, Nefedov, 1936), and probably less explicitly by a number of followers of the American school, that there is a greater specificity of qualitative composition of the vegetation cover to distribution of Acrididae than is accounted for by variations of microclimatic conditions due to structure of the vegetation. In a few cases, of course, this may be due to food preferences, but one would like to be more sure that the specificity is definitely greater than can be accounted for by microclimatic variation, before trying to think of any more recondite explanations for it.

As for the question of food as a possible limiting factor in distribution, the two detailed analyses of food preferences available, those of Rubtzov (1932) for Siberia and Isely (1938) for America, agree in showing that for the great majority of species preferences for food-plants are

well marked but not rigid or exclusive. Isely records a few species, particularly of the CYRTACANTHACRINAE, which have exclusive preferences, and consequently are associated with absolute plant indicators, but there are certainly no such examples known among the ACRIDINAE investigated and the nature of the food available is not likely to be a general limiting factor. Whether the amount of food available is likely to be limiting raises the question of the level of abundance likely to be reached ; records for the areas of maximum abundance of locusts or swarming grasshoppers show that the vegetation tends to be thin and irregular, while denser vegetation around supports much lower concentrations of grasshoppers (*e.g.*, Uvarov, 1928, 1932, 1933 ; Rubtzov, 1932*a*). In the temperate latitudes of Western Europe, where such high concentrations are not found, it is very probable that food supply is never a limiting factor.

The possibility that limiting factors may vary with the general level of abundance is not to be lightly dismissed, however. The concept of a saturation level of occupation of an ecological niche is very important in the interpretation of fluctuations of animal numbers, and this interpretation is likely to be concerned with different controlling factors according to the level of saturation. There are some authors (*e.g.*, Nicholson, 1931) who hold that such factors as macro- or microclimatic conditions may determine presence or absence of a species in a given niche, but that the important factors determining level of abundance are the activities of predators or parasites, with food supply and competition for the same niche determining saturation level. The arguments and mathematical demonstrations that Nicholson uses are based on excessively simple assumptions, and the relative importance of these various factors must vary widely with the groups of animals considered. In the case of ACRIDIDAE it seems likely that local climatic conditions are more important than other factors not only in determining limits of habitat tolerance, but also in contributing to fluctuations of abundance. With other animals less closely related to the local peculiarities of vegetation cover—for instance with a greater range of normal movement, with a partly subterranean existence, or with a less exclusively vegetable diet—local climatic conditions might well be expected to be less important, and the considerations advanced by Nicholson more valid. Nevertheless it would be unwise to scout the importance of predator or parasite relations for the massive fluctuations of ACRIDIDAE ; in a few cases an increased incidence of attack has been noticed during a period of increased abundance—*e.g.*, high incidence of parasitism of egg-pods of *Arcyptera microptera* (F. W.) by *Mylabris* (Rubtzov, 1932*a*).

Another limiting factor for ACRIDIDAE is the occurrence of conditions suitable for reproductive activity, namely for deposition of eggs and survival of eggs and nymphs. Uvarov (1928 and since, *passim*) has emphasised the importance of the sensitivity of nymphs rather than adults to climatic conditions, as the crucial factor for survival of the species. It is well known that breeding conditions are less abundant and widespread than localities suitable for adults (Vestal), and there is evidence for localisation of suitable conditions for egg deposition and

survival (*e.g.*, Uvarov, 1932, 1933; Rubtzov, 1932*a*; Nefedov, 1933) connected essentially with properties of the soil. Rubtzov (1932*a*) described interesting examples of optimum habitats with local juxtaposition of areas suitable for egg laying and areas with dense plant cover providing more food.

The question of ecological plasticity of Acrididae is very interesting, and of great economic importance; it is essentially plasticity in relation to climatic conditions. Qualitative observations on the subject have been made by nearly every worker recording distribution of individual species, and deducing therefrom differences of ecological requirements; important points are the wide range of tolerance of environmental conditions shown by many economically harmful species (especially emphasised for the swarming grasshoppers of Siberia by Rubtzov, 1932*a*), and the common, but not invariably high, plasticity of species with a wide geographical distribution. The quantitative work of Gause (1930, 1932) and Franz (1930, 1933) on a few species is interesting as an attempt to produce a fairly precisely comparable index of ecological plasticity for different species. Gause's attempt is the more ambitious, but is disappointing on several grounds—numbers of individuals observed and information about experimental technique are scanty; method of recording vegetation in terms only of the mass scythed from a given area is gross; and the value of relating precisely the cocked-hat distribution of his curves of population density against temperature and evaporation, based on very few observations, to a normal distribution, is very questionable; such simplifications in an effort to characterise mathematically complex systems controlled by so many variables is hardly likely to be of any value. The more limited comparisons of Franz (1930), of limits of temperature toleration of a few species, are much more successful.

Besides the greater ecological plasticity of species with wide geographical distribution, there is another important feature of habitat preference in relation to geographical distribution. Bei-Bienko (1930) described a definite variation of the type of vegetation preferred by particular species, over a range of four geographical zones of vegetation, such that a species definitely mesophilous or hygrophilous in the south would be more xerophilous in the north; he interpreted this as showing constancy of range of preference of microclimatic conditions even when, as a result of geographical variation, these are provided by different plant associations.

After this account of particular features of the autecology of Acrididae, it may be well to consider shortly the various community studies. It has already been mentioned that such work, of the type of descriptive surveys, is at least an important preliminary to more detailed ecological investigation, but it is safe to say that the greater the range of species and habitats surveyed, and the greater the variety of life-histories and habits involved, the more must the methods used lose preciseness and become liable to subjective modification and error. Thus for treatment of a fauna of Orthoptera much more varied methods of observation will be necessary than if the investigation were confined to Acrididae only, and the observations will be correspondingly lacking in comparability

and thoroughness of detail. The surveys of La Baume (1912, 1920), Zacher (1917), Fruhstorfer (1921), Salfi (1924), Kozminski (1925), Medvediv (1928), Grassé (1929), Randon (1932), Strohecker (1937), and Cantrall (1943), have dealt with other families of Orthoptera besides ACRIDIDAE, with consequently less detailed results than would have been possible with a more restricted field of work. It is not difficult to compile lists of species which are characteristic of various habitats distinguished by vegetation, soil or climatic conditions. These lists are then dignified by the name of associations, though often the only connections traceable between its members are those of systematic relationship and spatial proximity; their true ecological relations may be only of the most superficial, and often are no further analysed. Thus in a given plant association there may be recorded species of TETTIGONIIDAE inhabiting the branches of trees and shrubs, species of ACRIDIDAE inhabiting the soil and herbage of grassy enclaves or bare stony areas, and species of GRYLLIDAE and BLATTIDAE living among the leaf debris beneath the trees and shrubs. Now the species are ecologically related in so far as they find the right conditions for their occurrence in one or other stratum of a habitat which has some unity and ecological coherence; but the points by which the unity of this plant association is judged may not be in the least significant as the ecological factors determining the occurrence in it of the various Orthoptera—they may, for instance, concern the successional relationships of the plant association. It is not intended to belittle the consideration of the vegetation of a habitat for its own sake, in animal ecology; but to emphasise the need for considering its detailed structure in relation to the habits and life histories of the animals concerned—in other words, for recognising the differentiation of a plant association into many different habitats for different types of animal, each with its own microclimate, and each related to a particular community of animals, united not by systematic relationship but by their direct and indirect dependence on the environmental conditions provided by that microclimate. There is nothing new in this contention—in theory all ecologists recognise its validity; in relation to ACRIDIDAE, it has long been maintained by Uvarov (*e.g.*, 1928, 1932, 1933) that practical ecology should take more account of it, while Vestal (1913) has already been cited as holding that the environment should be studied in relation to the distribution of the factors important in the biology of the animals concerned. The importance to be attached to local climatic conditions of course varies greatly with different animals, particularly in relation to mobility and feeding habits; but in the case of relatively stationary phytophagous insects like ACRIDIDAE it is definitely high. An ecological association of animals must primarily be considered in the light of all those features of the environment and of the interactions of its component members which are directly related to the ecological requirements of every individual member; the essential criterion for recognition of an association must be to establish evidence of such ecological relatedness, and it is putting the cart before the horse to draw up a list of systematically related species inhabiting a particular habitat, and afterwards to try to trace more detailed ecological relation-

ship between members of this association—in many cases the relationship goes no further than this point. One may work through a given systematic group in order to determine the local distribution, and the individual habits and requirements of its members ; but the associations into which they should then be fitted should depend on the discovery of the particular aspects of the local conditions to which each is related ; then an association will consist of the animals (not necessarily systematically connected) which have a common relation to some or all of these particular local conditions, and show interactions of ecological significance. Criticism of this sort is to a large extent a counsel of perfection, and in practice a thorough application of these principles would involve much delay and hard work before one could begin to see the wood for the trees in complex ecological systems ; superficial surveys are necessary and it is convenient first of all to assign groups of animals roughly to the broader subdivisions of types of environment, before going into their ecology in detail. The important point is that the incompleteness and provisional nature of such a course should be recognised, and that it should be accepted that detailed study of each member of an association from the autecological point of view must precede full interpretation of its synecology—that is, of its role in the association as whole. Difficulties in applying this point of view should not be lightly dismissed ; they are not only those of the great deal of hard work to be done, but also those involved in one's æsthetic attitude to the work, which to many ecologists is a most important factor. Many have arrived at the serious study of ecology via a general interest in living things and the attraction of the subject lies in its combination of intellectual interest with æsthetic satisfaction. This æsthetic satisfaction stems from the recognition of the manifold relationships shown by the living organisms which are presented to our sensory field ; that field is so constituted, however, that we tend to perceive living things in the sort of "association" in which connecting features are rather those of spatial proximity than of ecological relatedness. There is consequently a tendency for our æsthetic appreciation to be too easily and fully satisfied by superficial observations taking primarily into account the factor of spatial proximity ; and this easy satisfaction may be the parent of a disinclination to pursue a further analysis by which the initial grounds for associating the members may be modified and even destroyed. It needs a persistent intellectual effort to continue the ecological analysis ; many will find the effort not worth while, and many more will not find time for it, but in the end slow and thorough analysis will yield the most satisfying results, both intellectually and æsthetically, even in very complex cases.

In considering the British Acridid fauna, advantage is taken of the fact that all the species of grasshopper are common (though not necessarily widely distributed), fairly closely related, and of similar habits and life history. They form a uniform group whose general autecology may profitably be considered, and at the same time show interesting minor differences of habitat preference. It is proposed here mainly to analyse the composition of vegetation in the habitats in which

they occur, to determine the degree of their localisation to particular features of the vegetation, and to try to relate their habits and ecological requirements to this localisation.

## Methods in Grasshopper Recording.

### *Estimation of Abundance.*

This work was begun with the firm intention of using quantitative methods to as great a degree as practicable. The difficulties of deciding the relative merits of numerical and subjective methods are, however, many and complicated. The outstanding disadvantages of subjective methods are the difficulty in comparing results of different observers, and the strain on the efficiency and integrity of the observer. If standards used are purely subjective, then one man's observation can never be readily comparable with another's unless each has personal experience of the other's use of his system. Also the use of any method is subject to errors due to observers' fatigue and similar factors, and the more a method is based on subjective judgment the greater will be its liability to disturbance by such errors. As for integrity, this must be considered on a subconscious as well as a conscious plane; it is a poor investigator who is not interested in his results, with a frequent tendency to bias in favour of one of several possible working hypotheses, and even with the best intentions it is very difficult to avoid the distortion of subjective judgment by such bias, at least in a subconscious way, which is the more dangerous in that it may not be suspected.

Objections to numerical methods, on the other hand, are that without careful analysis and control of the condition under which they are used they may give a sense of spurious exactness, and that as the number of variable factors involved increases, the difficulty of application of a numerical method increases in geometrical proportion, since simultaneous control or alternatively analysis of many variables is extremely complex. Conditions must therefore be simplified and controlled as far as possible, but field work commonly involves many variable factors difficult to control. The advantages of numerical estimations carefully performed are, however, so definite that it is well worth examining how far such methods can be applied.

Many workers, such as Vestal (1913), Isely (1937), Cantrall (1943), have described the variety of behaviour, environmental localisation and habits of different Orthoptera or of different Acrididae; to quote Isely, "Activities of flying, whirring, stridulating, jumping, ducking, sliding, slinking, sneaking, dodging, freezing and colour flashing are as characteristic of grasshoppers as similar activities are characteristic of birds and other vertebrates." While the distinction between sliding, slinking and sneaking seems subtle to the point of tenuousness, it is clear that an experienced field observer's knowledge of these habits enables him to make subjective comparative estimations of abundance in conditions too varied for comparative numerical estimation. There is thus a *prima facie* case for subjective methods in dealing with a wide variety of species, and Cantrall (1943), for instance, used a single graded subjective scale of abundance for his large and varied fauna. As already mentioned,

however, there is a good case for concentrating on the ecology of more limited groups of species with fairly similar habitat preferences, and quantitative estimates can be made more practicable by such restriction of variables. Most workers have made their estimates more or less quantitative, even in spite of stressing the importance of the judgment of an experienced field worker (*e.g.*, Isely, 1937). There is, however, a great diversity in the various methods of quantitative and semi-quantitative estimation, and some of them give information of only limited value.

Vestal (1913) described modification of a simple sight count by subjective judgment according to experience of habits of different species, to give indications of both abundance and constancy of occurrence on a verbal, non-numerical scale. Kozminski (1929) classified species rather on their range of habitat occupation and constancy in each habitat, and did not consider the question of absolute abundance. Grassé (1929) and Bei-Bienko (1930) made quantitative sample counts, whether by sight or by hand or by sweep-net collecting, but deduced only relative abundance of the different species from these figures, and not absolute numbers. Gause (1930) used the quantitative method of time-catches, with hand-collecting, estimating abundance as numbers of individuals taken per unit of time. Diver and Diver (1933) used hand collecting and sweeping methods, and expressed their results variously as quantitative records, as percentage abundance of different species in a total catch, or as actual sample numbers, according to particular exigencies. Isely (1937) used sight counts, net records and so-called mass collecting as a quantitative basis for a complex empirical method of working out an abundance index for each species in a given habitat. This list serves to show very clearly the variety of methods used by previous workers, but three general conclusions can be drawn from comparison of these methods. The first is that methods for estimating relative rather than absolute abundance are less liable to error and are simpler, but give less informative results, and their use still needs considerable care; the second point is that as methods become more numerical so they are progressively more informative; and the third is that the need to introduce subjective elements into estimation methods increases with complexity of conditions studied.

Adoption of suitable methods involves considering the nature of the problems to be investigated, cutting down as far as possible the number of uncontrolled variable factors influencing estimations, and then selecting from among the available methods the most informative ones compatible with the need for simplicity that limited time for working imposes on the choice.

The primary need is for a simple method for numerical estimation of absolute abundance, suitable for routine comparative work over a range of habitats. The difficulties and sources of error are—

(1) The wider the range of habitats, and the greater the differences of local distribution of the various species within a habitat, the greater the possible error due to difficulties of searching and collecting.

(2) The habits of individual species may vary at different seasons of the year, in different weather, at different times of the day; and error will again be introduced if the effect of this variability on the result is uncontrolled.

(3) The more complex and variable the factors involved, the greater is the observer's liability to errors due to fatigue or inaccuracy.

The error due to factors of category (1) is less in the case of British fauna than in some of the more general surveys, since only a relatively uniform group of species is dealt with. It is correspondingly more worth while to cut down variability due to factors of category (2) by standardising times and conditions of observation, and so to increase the possibility of a reasonably exact and simple quantitative method.

Possible methods available are sampling—by sweeping or individual collecting; counting all specimens in sample areas; or use of the method of dilution of marked individuals in the population.

*Sweeping.*

Limitations of the method relate to the observer's thoroughness, the mechanical difficulties imposed by variations in structure of the vegetation swept, and variations in distribution and activity of the insects concerned according to the seasonal and climatic factors, etc. Under standard seasonal and climatic conditions sweeping is a useful method for taking samples from grasshopper populations over not too wide a range of structure of the vegetation inhabited, provided differences due to relative activity of, say, nymphs and adults, or males and females, are observed and if necessary allowed for. It is a useful method for taking routine samples—*e.g.*, to test distribution of colour variations among different populations. The mechanical difficulties imposed by varying vegetation structure, however, preclude any possibility of such samples bearing a standard relation to the total number of the population, and this, combined with the other sources of variation—activity and local distribution—makes the method unsuitable for absolute numerical estimation, at least in comparing different habitats.

*Other methods of mass collection.*

Methods in which care of the observer can more efficiently compensate for the difficulties of variation of vegetation structure or activity of the insects are those in which individual capture by net or hand is used instead of sweeping. The most successful quantitative way of using them is to determine the total catch in a given time over a given area, and if the results can be checked against occasional more detailed estimation of absolute numbers by another method, this time-catches method gives reliable estimates of absolute concentration suitable for routine work; even if this standardisation against absolute estimations is not made, it is still a good method for comparative observations. It does demand care and alertness on the part of the observer, however, to a greater degree than does sweeping, and these demands increase with the wider range of conditions observed; a fixed, conventional routine of capture is necessary to avoid bias in attempts to sample uniformly

habitats of diverse vegetation structure or populations of individuals of varying activity.

*Direct estimation of numbers per unit area.*

None of the above sampling methods is strikingly simple to use, and unless checked against some method of absolute estimation they are in any case only of comparative value, and that only for a single investigation. For high concentrations and a uniform grassland habitat the advantages of a simple square metre count are obvious, and a standard net-covered frame of this size was used. But for low densities over larger areas sight counts are more suitable.

*Observations of Behaviour.*

Besides the estimations of abundance of individuals just described observations were made on motility and on feeding habits. In the observations on motility considerable time was spent watching behaviour in natural conditions of unmarked individuals, or ones with a distinguishing mark of oil paint on the pronotum (as used for the recapture frequency experiments), and the distribution of marked individuals liberated in a particular area was followed at intervals after the liberation. For the feeding observations most use was made of watching grasshoppers feeding under natural conditions, or confined under inverted two-pound glass jam-jars in their natural habitat or on a garden lawn.

By simple watching without any disturbance information has been gained about many aspects of behaviour (incidentally it is surprising that so little reproductive activity was noticed in spite of the long periods spent in watching), particularly about normal movements and feeding, and predatory activity of birds ; watching with some degree of disturbance has given information about motility of marked individuals, about effects on the behaviour of different types of disturbance, and about such special activities as autotomy. Watching is the most enjoyable method of work ; sample taking is laborious ; census taking often tedious ; but watching grasshoppers is a most congenial occupation for hot summer weather, with minimal exertion and with stimulation of interest and pleasure both by specific activities of the grasshopper and by the many other features of their habits (even though at times these are unable to compete with a tendency to go to sleep).

Marking for the motility experiments involved the same method and precautions as have already been described, and the details of place and time of recapture will be described with the results.

*Vegetation Recording.*

The quantitative methods available for description of plant communities are so laborious and time-consuming, and the methods of listing plant species according to a subjectively judged scale of abundance are so well established and relatively flexible for routine purposes, that there was no doubt that subjective methods would have to be used here.

The actual routine of description of vegetation is as follows :—

(*a*) List of the component species. This has been made fairly com-

plete, in the sense that phanerogams characteristic of the habitat are included unless they are rare ; species described as occasional or frequent may play a negligible part in the gross structure of the vegetation, and yet be so characteristic of a community of a given structure as to be a suitable indicator ; however, indicator species for grasshoppers are perhaps related more often to food preferences than to structure of vegetation, and since such grasshoppers as have food preferences are commoner among other subfamilies than the ACRIDINAE (Rubtzov, 1932 ; Isely, 1938), the prospects of finding indicator species for favourable habitats here are not great. Detailed lists for the various habitats are, however, also interesting from the point of view of the often subtle changes in composition associated with structural changes important for grasshoppers. Only the commoner mosses are included according to the degree in which they play a significant part in the structure of the grassland and related habitats considered here ; the only lichens with an important structural role are species of *Cladonia* and their identification has not been carried further ; liverworts, fungi and algae have not been found to be worth record (only for the present material, however ; work on TETRIGIDAE, for instance, might well need to take account of soil algae).

(*b*) Each of the species listed is characterised as dominant (symbol *d*), subdominant (*sd*), abundant or very abundant (*a* or *va*), frequent or very frequent (*f* or *vf*), or occasional (*o*). To any of these may be added the qualification locally (*l*), or more specifically marginally (*m*) ; for instance, a species may be described as *lf*, or *o-lf*, if it is generally occasional over the whole habitat, as well as locally frequent. As much of the investigation is concerned with the local differentiation of structure within communities, the qualification *l* will be used more often than is likely in routine observations on overall composition of the community, for the standards of localisation appropriate to grasshopper distribution are on a much smaller scale than those of general surveys of vegetation.

(*c*) The rough limits of height of the general vegetation are recorded, and an estimate is made of the percentage vegetation cover over the habitat as a whole. This estimate of cover is only very rough, within wide limits, and made subjectively, by inspection ; for the sake of simplicity, and of separating properties of the texture of the vegetation from the question of soil exposure, the amount of soil not covered was reckoned as that intervening between adjacent plants, and not that exposed between interstices of the meshwork formed by overlapping leaves of adjacent plants ; this latter interstitial exposure of soil between intercrossing leaves was taken into account in appraising thinness of texture of the vegetation.

(*d*) More or less detailed observations were made and recorded for each habitat on topographical features—exposure, slope, and local variations of contour ; on the properties of the soil, including possible local differentiation ; on general or local incidence of grazing, mowing, ploughing, etc. ; on general or local peculiarities of growth form or texture of the vegetation ; and on any miscellaneous features of importance. Most of these, of course, cannot be reproduced here *in extenso*, but they contribute to the analysis and description of habitats.

## VEGETATION AS A HABITAT.

### *Height and Density.*

Height and density of the vegetation are probably the most important

features for grasshoppers. In Table 1 all the habitats investigated are tabulated according to rough limits of density (expressed as percentage vegetation cover) and height of vegetation, and according to a rough estimate of abundance of grasshoppers (in number of adult individuals per square metre). The frequency with which each type of vegetation supports populations of grasshoppers of the various densities can be seen. The separation only of wider groups of concentration of grasshoppers per square metre was dictated by convenience and by the factors limiting the accuracy and validity of a single determination of the population of a habitat (in most cases only a single determination was possible). As regards heights of vegetation, those uniformly greater than 20 or 60 cm. were only found where the cover was 100 per cent.; for each category with cover less than 100 per cent. only two subdivisions have been recognised — height less than 20 cm., and mixed composition with some components more than 20 cm. high.

The table show that the types of habitat most frequently met with were those designated 100 per cent. cover and 5–20 cm. height, 100–80 per cent. $< 20$ cm., and 80–50 per cent. $< 20$ cm. Of these, the two latter show the greatest proportion of high grasshopper densities, but the range of all three is very similar. 100–80 per cent. mixed $>$ and $< 20$ cm. was a category less often observed, but with a good proportion of high densities; 80–50 per cent. mixed $<$ and $> 20$ cm. shows even fewer records, but again these are largely of good densities. On the other hand, 100 per cent. 20–60 cm. and 100 per cent. $< 5$ cm. were fairly often observed types of vegetation, but usually with poor densities (the one anomalous high record for each will be further discussed later). The other vegetation types were less common, and of comparatively trivial importance; 100 per cent. $> 60$ cm. was a uniformly unfavourable type of habitat, with never more than casual individuals to be found, whole 100 per cent. mixed $>$ and $< 60$ cm. and the types with low percentage cover were not so uniformly unfavourable, though only occasionally observed. It may be concluded that incomplete vegetation cover, between 50 and 100 per cent., of a height less than 20 cm. (whether uniformly less or in association with some higher vegetation), is most favourable to the grasshoppers considered here; the range of tolerance, however, is much wider.

Conclusions from such a table are very broad and approximate. In the first place, although it was attempted to survey a fair sample of all the types of grasshopper habitat, there is a natural bias towards more numerous records of the more favourable; within each individual vegetation type records have been made independently of the grasshopper concentration found, but naturally relatively less attention has been paid to the unfavourable habitats; these factors of possible subjective bias should be borne in mind. Second, and more important, in a general table justice cannot be done to all the factors involved in the structure of the vegetation, and more detailed consideration of these is needed. The preference for habitats with discontinuous cover, and perhaps considerable further local differentiation of structure, demands analysis of local structure as well as general composition of vegetation.

TABLE 1.

Vegetation structure and densities of adult grasshoppers.

| Vegetation | | Adult density per sq. metre. | | | | | | | Adult density per sq. metre | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Per cent. cover | Height, cm. | 0–0·1 | 0·1–0·3 | 0·3–1 | 1–3 | 3–6 | 6–10 | >10 | 0–0·1 | 0·1–0·3 | 0·3–1 | 1–3 | 3–6 | 6–10 | >10 |
| | | | *All species together* | | | | | | | *Omocestus viridulus* | | | | | |
| 100 | <60 | 5 | | | | | | | 2 | | | | | | |
| 100 | > and <60 | | 3 | | 1 | | | | 1 | | | | | | |
| 100 | 20–60 | 6 | 4 | 1 | 3 | | 1 | | 4 | 3 | 1 | | | | |
| 100 | 5–20 | 7 | 8 | 10 | 5 | 5 | | | 15 | 1 | 2 | | | | |
| 100 | <5 | 8 | 2 | 1 | 1 | | | 1 | 3 | | | | | | |
| 80–100 | > and <20 | | 2 | 4 | 7 | 2 | | | 1 | | | 1 | | | |
| 80–100 | <20 | 5 | 2 | 5 | 12 | 6 | 3 | | 8 | | | | | | |
| 50–80 | > and <20 | | 1 | 2 | 3 | 1 | | | | 1 | | | | | |
| 50–80 | <20 | 2 | 5 | 4 | 9 | 3 | | | 1 | | | | | | |
| 20–50 | > and <20 | 1 | | | | | | | | | | | | | |
| 20–50 | <20 | 1 | 2 | | | 2 | | | | | | | | | |
| 0–20 | | 2 | | | | | | | | | | | | | |
| | | | *Chorthippus bicolor* | | | | | | | *Stenobothrus lineatus* | | | | | |
| 100 | >60 | | | | | | | | | | | | | | |
| 100 | > and <60 | | | | | | | | | | | | | | |
| 100 | 20–60 | 5 | | | | | | | 2 | | | | | | |
| 100 | 5–20 | 10 | 3 | 5 | 3 | | | | 5 | 1 | 1 | 1 | | | |
| 100 | <5 | 6 | 2 | | | | | | 1 | 1 | | 1 | | | |
| 80–100 | > and <20 | | 1 | 5 | 3 | | | | 1 | | 4 | 1 | | | |
| 80–100 | <20 | 7 | 8 | 7 | 15 | 2 | | | 2 | 2 | 4 | 1 | | | |
| 50–80 | > and <20 | | 2 | 3 | 1 | 1 | | | | | | | | | |
| 50–80 | <20 | 5 | 6 | 2 | 7 | 1 | | | 1 | 2 | 2 | 1 | | | |
| 20–50 | > and <20 | 1 | | | | | | | | | | | | | |
| 20–50 | <20 | 2 | | | 2 | | | | | | | | | | |
| 0–20 | | 1 | | | | | | | | | | | | | |
| | | | *Chorthippus parallelus* | | | | | | | *Gomphocerippus rufus* | | | | | |
| 100 | >60 | 4 | | | | | | | | | | | | | |
| 100 | > and <60 | | 3 | | 1 | | | | | 2 | 1 | | | | |
| 100 | 20–60 | 8 | 2 | 3 | 6 | | | | 2 | 3 | | 1 | | 1 | |
| 100 | 5–20 | 7 | 8 | 7 | 8 | 2 | | | | 5 | 3 | | 1 | | |
| 100 | <5 | 5 | 1 | 1 | 1 | 1 | | | | 2 | | | 1 | | |
| 80–100 | > and <20 | | 2 | 4 | 4 | 4 | | | | 2 | 1 | 3 | | 1 | |
| 80–100 | <20 | 6 | 1 | 6 | 9 | 3 | 1 | | | 2 | 1 | 3 | 2 | | |
| 50–80 | > and <20 | | | 1 | 1 | | | | | | | 1 | | | |
| 50–80 | <20 | 2 | 6 | 5 | 3 | | | | | 2 | 3 | | 1 | | |
| 20–50 | > and <20 | | | | | | | | | | | | | | |
| 20–50 | <20 | | 2 | | | | | | | | | | | | |
| 0–20 | | | | | | | | | | | | | | | |
| | | | *Chorthippus albomarginatus* | | | | | | | *Myrmeleotettix maculatus* | | | | | |
| 100 | >60 | | | | | | | | | | | | | | |
| 100 | > and <60 | | | | | | | | | | | | | | |
| 100 | 20–60 | | | 2 | | | | | | | | | | | |
| 100 | 5–20 | 1 | | 2 | 1 | 1 | | | | | | | | | |
| 100 | <5 | | | | | | | | 1 | | | | | | |
| 80–100 | > and <20 | | | | | | | | | | | 1 | | | |
| 80–100 | <20 | 3 | 1 | | 1 | | | | 1 | | 2 | 5 | 1 | 1 | |
| 50–80 | > and <20 | | | 2 | | | | | | | | 2 | | | |
| 50–80 | <20 | 1 | 1 | 2 | | | | | 2 | 4 | 1 | 3 | | | |
| 20–50 | > and <20 | | | | | | | | | | | | | | |
| 20–50 | <20 | | | | | | | | | | | 1 | | | |
| 0–20 | | | | | | | | | | | | | | | |

The degree to which the total range of tolerance of vegetation types shown by all species is influenced by varying preferences of different species may be seen by comparing the records of occurrence of each individual species (except *Omocestus ventralis*, of which only three observations have been made). A general similarity between species is obvious, but *Chorthippus parallelus* and *Gomphocerippus rufus* constitute more records to the denser vegetation types, for instance, than do *Chorthippus biedor* and *Myrmeleotettix maculatus*.

### *Properties contributing Shelter and Warmth.*

In general, vegetation which is of dense texture or tall is not readily warmed by the sun, nor so readily cooled by free circulation of air, as is thin vegetation. Density is consequently desirable for shelter, though the need for it may be modified by topographical considerations such as aspect in relation to the sun, slope and configuration of surrounding physical features of the landscape. Thin vegetation, however, provides better conditions for diurnal activity in favourable weather, though the physical features of the habitat just mentioned are again important, with the additional one of the thermal properties of the exposed soil. It is not surprising, then, that many favourable habitats show local differentiation involving areas of denser vegetation sheltering and perhaps surrounding sparser areas with some exposure of bare earth: even in habitats with a generally fairly high population of grasshoppers it is usual to find locally higher densities in such sheltered and readily sun-warmed parts, while in habitats which on the whole show unfavourable physical or vegetational features the limitation of individuals to such occasional suitable areas is often striking. Hence it may be well to examine what components of the vegetation contribute to the favourable or unfavourable aspects of structural differentiation.

Percentage cover is not the only important aspect of density of vegetation. It determines one significant thermal property—the amount of sun-warmed soil: but it does not take account of the other important factor—the texture of the three-dimensional meshwork of vegetation. Texture is determined by the growth-forms of the component plants—leaf form and distribution, and overall height: and the main environmental factors determining these are water content and structure of the soil (involving such factors as drainage, slope, and chemical composition of the subsoil), exposure to sun and wind, and biotic interference (*e.g.*, treading of paths or grazing of pastures). Let us analyse the pattern of growth-forms shown by the habitats considered here—heath or waste land, grassland, and scrub, with their various intercombinations.

Three main levels of vegetation may be recognised, in varying degree, in these types of vegetation. I do not use the term formation, as I am not considering whole formations for their own sake, but only for what may be found in them relevant to grasshopper distribution. The validity of this position is recognised in practice, but I should like to make a plea for its theoretical recognition too: the ecologist should be able to acknowledge and investigate the fundamentally important question of the interrelations of plants and animals as mutually dependent members

of the same biological community without being obliged to recognise and apply to his study of the animals such theoretical and polemical concepts as the relation of communities of vegetation of very varied structure to a given climax or series of climaxes, or the essential unity of vegetation formations characterised by similar climatic and edaphic conditions in spite of considerable local topographical diversity. Correlation with such broad general aspects of vegetation may be of value in dealing with distribution on the geographical scale (*e.g.*, Bei-Bienko, 1930) or in considering larger animals with a wide range of movement ; but it should rest with the animal ecologist to select those aspects of similarity and diversity of types of vegetation crucial to the animals he is studying, independent of purely botanical considerations.

Of the three layers to be described, the first is scrub layer, characterised by woody shrubs or herbaceous species of tall or straggling and diffuse habit ; this was rarely or never found to be uniform and continuous, but was more or less intimately mixed with areas showing nothing taller than the second or herbaceous layer, which was numerically and qualitatively by far the most important layer for suitability of habitat. Third is a layer not constantly found, composed of mosses and small herbs below the general level of the second—it is best developed in habitats in which the second layer is moderately dense and tall. The various vegetation categories of Table 1 may profitably be analysed in terms of their relative proportions of these layers, and of the factors concerned.

Of the three categories with vegetation cover less than 50 per cent. little need be said ; the few records are of fallow or stubble fields with the characteristic casual weeds of arable land, or of fairly well-used tracks in which continual use prevents the encroachment of the marginal scrub or grassland, or of stony slopes among chalk grassland. Where such areas are at all extensive the conditions are unlikely to be favourable to occurrence of permanent breeding populations of grasshoppers, independently of structure of the vegetation, for in each case the soil conditions are not favourable to deposition and survival of eggs, whether because of ploughing, repeated treading, or excessive stoniness. On the other hand, local areas with cover less than 50 per cent. may be very common in habitats which are in general more densely grown—for instance, in discontinuous Callunetum with interstitial *Deschampsia flexuosa*, *Agrostis tenuis*, *Potentilla erecta*, *Polytrichum juniperinum*, *Galium saxatile*, and *Hypnum cupressiforme*, common on the sandy heaths of S.E. England, or in thin stony Festucetum ovinae on the chalk, with local areas of increased stoniness, showing *Carex flacca*, *Helianthemum vulgare*, *Cladonia* spp., and *Camptothecium lutescens* or *Ceratodon purpureus* and *Dicranum scoparium* prominently ; in these cases there may be a marked concentration of, say, 1–3 individuals of *C. bicolor* or *M. maculatus* per square metre in the sparsely covered areas, during diurnal activity, while the association as a whole may show a density of 0·1–0·3 per square metre or less. In general, then, vegetation with less than 50 per cent. cover which is easily warmed and cooled on account of the general thinness of cover is unlikely to provide a good habitat

for grasshoppers: on the other hand, when it occurs locally among richer vegetation it may be a very suitable habitat for diurnal activity of grasshoppers, fond of warm, dry earth, while shelter against hard weather is provided by surrounding denser growth. It will be interesting to trace to what degree the denser habitats owe their suitability for the various species to such local sparse areas.

In passing to the categories with 80–50 per cent. and 100–80 per cent. cover there is obvious an increasing clearness of differentiation of the three layers described, which reaches a maximum among habitats with 100 per cent. cover. The scrub layer, of course, will not be expected to be present in herbaceous or true grassland associations, though herbaceous associations may show species in the main herbaceous layer characteristic of scrub rather than of true grassland, which may alter conditions significantly (*e.g.*, chalk scrub and chalk grassland). The main importance of scrub components lies in the irregularity of structure and consequent diversification of microclimatic conditions that they contribute. Especially when they are dense (*e.g.*, *Ulex europaeus* bushes) they form good shelter on the sun-warmed sides of which, among thinner vegetation, conditions are especially favourable for grasshoppers; loose straggling scrub, on the other hand (*e.g.*, of *Rubus fruticosus agg.*, *Rosa* spp., *Clematis vitalba*) may itself provide suitable conditions for those species which live more readily on vegetation of the order of 20–30 cm. from the ground or more. *G. rufus* and *C. parallelus* are such comparatively more phytophilous species, and an examination of Table 1 shows that records for the 100 per cent. cover category routinely including a scrub layer (100 per cent. mixed $>$ and $<$ 60 cm.) are almost all confined to *G. rufus* and *C. parallelus*: in this category cover is too dense and continuous for the factor of sheltering more thinly vegetated areas to be important. On the other hand, records for categories 100–80 per cent. mixed $>$ and $<$ 20 cm., and 80–50 per cent. mixed $>$ and $<$ 20 cm. show that both factors are operating, and that conditions simultaneously favour the more phytophilous *G. rufus* and *C. parallelus*, and the more geophilous *C. bicolor* and *M. maculatus*. It perhaps hardly needs emphasising that neither of these factors (nor indeed any other single factor to be discussed) is necessarily limiting, and that all the species mentioned may flourish in habitats with no scrub layer at all. Furthermore, the life history of all these species is very similar, and though *G. rufus* and *C. parallelus* are comparatively phytophilous, their eggs must be laid in the ground in the same way as those of other species, so that an important part of their activities must be carried on on the ground among fairly thin vegetation and in soil of suitable consistency. Thus even the most phytophilous species need some irregularity of the scrub layer with intermixing of shorter and sparser growth. A possible objection may be considered to the small proportion of records including scrub components among habitats with 100 per cent. cover, compared with the higher proportion among habitats with 100–80 and 80–50 per cent.: the reason for this is that scrub with 100 per cent. cover is comparatively uncommon in S. England. A number of records of 100 per cent. vegetation cover uniformly taller than 60 cm. have been made

(Table 1), but they are all of particularly luxuriant types of grassland ; if a special effort has been made to find similarly dense habitats with scrub components there seems no reason to suppose they would have been any more favourable to grasshoppers.

The herbaceous layer is by far the most important and variable one of this range of habitats examined, and as the third or under-layer, mainly composed of mosses, varies in a manner closely related with the variation of the former, they may well be considered together. The common variations in height, density, texture and uniformity may be related to the following factors :—

(1) Nature of component species.
(2) Properties of the soil—notably texture, water content, acid-base balance and content of nutrient substances.
(3) Local topographical factors of slope, exposure to sun and wind.
(4) Grazing, and other biotic factors, such as treading.

Not all of these are of equal importance. Factors concerned with the general poverty or richness of the soil largely determine the richness of the vegetation ; grazing and treading affect the general richness and also the growth-forms of the component plants ; degree of shading or exposure to sun has effects on density and especially on the amount of development of the moss layer. The nature of the component species is important mainly so far as it depends on these determinants of density and growth-form ; within fairly wide limits associations of similar structure but of very different component species, on soils of different acid-base status, for instance, are apparently equally suitable for the same species of grasshoppers (*e.g.*, the indifferent occurrence of *M. maculatus* on thin heathy grassland over sand, on chalk heath, or on thin basic chalk grassland). However, to begin by considering the main dominant species of the types of grassland met with, there are some which in full development are 60 cm. or more high (*e.g.*, *Arrhenatherum elatius*, *Dactylis glomerata*, *Agropyrum repens*, *Deschampsia caespitosa*, *Molinia caerulea*, *Juncus* spp.), and whose combination of height and density are exclusive of all but casual grasshoppers ; some of the order of 30–60 cm. (*e.g.*, *Bromus erectus*, the mixed grasses of neutral meadows, *Brachypodium pinnatum*), equally dense, and almost equally exclusive in maximum development ; and some up to 30 cm. (*e.g.*, *Festuca rubra*, *Lolium perenne*), less unfavourable, but still too uniformly dense for suitable breeding conditions. Passing now from these dominant types under good conditions, with relatively few associated species, to poorer soil conditions, three tendencies become apparent—first, the dominant species become less tall and less dense ; second, associated species become more varied and more abundant, so that thinner, more irregular vegetation appears, and the percentage cover falls ; third, new dominant species appear (*e.g.*, *Festuca ovina*, *Agrostis tenuis*, *Deschampsia flexuosa*), which only flourish in these thinner and poorer conditions, being unable to compete in good conditions with the more vigorous dominants already mentioned. In this transition to poorer ground the thinning, irregularity and increasing tendency to discontinuous cover all favour grasshoppers ; if one type

of habitat can be specified as particularly characteristic of them it is thin grassland on poor soil. Poor soil is, however, not the only important factor in providing such changes in grassland ; grazing and treading may also do so, but at the same time they may also produce very characteristic changes in growth form of the herbaceous layer, which are very important from the point of view of grasshoppers. Excessive grazing by rabbits, which is found mainly on the poorer soils, as in heathy or thin chalk grassland, tends mainly to promote thinness and irregularity of vegetation, with discouragement of the more vigorous species intolerant of poor soil or continual checks to growth, and encouragement of the grass dominants of thin grassland (such as *Festuca ovina*, *Agrostis tenuis*) and of more specifically rabbit-resistant plants (such as lichens—mainly *Cladonia* spp. ; mosses—*e.g.*, *Hypnum cupressiforme*, *Camptothecium lutescens*, *Polytrichum juniperinum* and *P. piliferum*, etc. ; and a few vigorous herbs or scrub species—*e.g.*, *Nepeta glechoma*, *Urtica dioica*, *Sedum acre*, *Ranunculus repens*, *Iberis amara*, *Cynoglossum officinale*, *Sambucus nigra*, *Juniperus communis*, *Rubus fruticosus agg.*). Many of the records in the 80–50 per cent. and 100–80 per cent. categories of Table 1 are habitats in which these effects of rabbits are important in producing discontinuity and local irregularity of cover, to which the suitability of the habitats is mainly due. Grazing due to farm animals has a strikingly different effect, however ; nearly all the examples of it were found on better soil, and the amount of grazing permitted was not excessive ; under such conditions there is a general tendency to production of a characteristic short, dense turf of neutral grassland species with a high proportion showing typically rosette or prostrate habit—the typical grasses, such as *Lolium perenne*, *Agrostis alba stolonifera*, and *Cynosurus cristatus*, become more and more horizontally spreading, and rosette species are prominent, such as *Bellis perennis*, *Hypochoeris radicata*, *Plantago media*, with others also showing horizontal disposition of broad leaves, such as *Prunella vulgaris*, *Ranunculus* spp., *Trifolium repens*. Where the cover is uniform, this vegetation is too dense to favour grasshoppers, and most of the records in the category 100 per cent. $< 5$ cm. of Table 1 are of this type of structure. The other factor producing such a structure among the present records is a constant not too heavy pressure by treading, met with among grassy tracks and moderately used paths through fields ; similar plant species usually tolerate such conditions (*Dactylus glomeratus* may also be added), but the effect of treading on firmness of the soil is an extra disadvantage to maintenance of permanent breeding populations of grasshoppers ; some of the low records in the 100–80 per cent. $<5$ cms. category are attributable to these effects of treading. On poor soil, of course, the amount of treading, or grazing, required to produce thinness and irregularity of vegetation is correspondingly less ; that the latter are so commonly the effects of rabbit grazing is probably due to this lower degree of tolerance shown by vegetation on poor soil, as well as to lack of control of rabbit pressure ; records of sheep pasture should show effects intermediate between those of horse and cattle and of rabbit grazing, but sheep pasture on the poorer soils is not common in the areas studied.

so there are no records of fairly dense uniform Festucetum ovinae or *Festuca ovina–Agrostis tenuis* pasture under moderate sheep grazing, such as might correspond to the 100 per cent. cover pasture of horses and cattle, and perhaps sheep too, just described for the better agricultural soils. Excessive grazing of any sort, of course, will eventually lead to thinness and irregularity of vegetation, perhaps with appearance of scrub components, including such grazing-resistant species as thistles, even on the best soil, and so favour the prevalence of grasshoppers; rabbits provide the best example here, but Treherne and Buckell (1922) for Canada, and Rubtzov (1932*a*) for Siberia, give accounts of similar effects on vegetation, with increase of grasshoppers to an extent where they themselves became an important means of pressure on the vegetation, initiated by over-grazing by domestic animals. Low intensity grazing on the best neutral soils will not produce the low, uniform dense-texture mat just described, but the resulting taller, less regular vegetation of finer texture is not much more favourable to grasshoppers, for the cover is still dense and complete. Low intensity grazing on soils second-rate or poor enough of themselves to favour thinner grassland with less regular cover, however, contributes an extra tendency to irregularity of structure which may further increase suitability for grasshoppers. Poor pastures subject to casual cattle grazing often show some local patches hardly grazed at all, while others are grazed to very variable degrees, and grasshoppers may congregate very strikingly on the lee or sun-warmed sides of the taller patches. A meadow of moderate richness on Oxford clay, recorded in Table 1 as 100 per cent. 5–20 cm., with a population of 3–6 per square metre—almost all *C. parallelus*—was subject to moderate grazing, and showed typical tall ungrazed patches here and there, around which the density of *C. parallelus* commonly rose from the general level of 3–6 to more than 10 per square metre, while scattered excessively close-cropped areas simultaneously showed densities of 1 per square metre or less ; in the taller areas such species as *Holcus lanatus*, *Dactylis glomeratus*, *Spiraea ulmaria*, *Chrysanthemum leucanthemum* were prominent, in contrast to *Scabiosa succisa*, *Trifolium repens*, *Ranunculus repens*, *Prunella vulgaris*, *Rumex acetosella*, *Primula veris*, *Potentilla reptans*, etc., in the shorter denser growth with poor grasshopper populations. Alternation of moderate grazing with the taking of one annual hay crop—a quite common practice in the agricultural grassland observed—also tends to produce a more varied structure, more favourable to grasshoppers, on good as well as poorer land, than does grazing alone ; this no doubt due to the taller less dense-textured growth permitted during the most important growing months of the year, and to the greater variety of species in combined hay-and-grazing grassland.

The last important factor in determining the importance of height and density is the amount of shade or exposure to sun. In associations with closed scrub or tree layer the resultant shade may have various effects on the herbaceous layer : the latter may be quite absent ; may consist of little but mosses ; may be a dense continuous layer of such species as *Mercurialis perennis* or *Sanicula europaea* ; or may have a

loose irregular structure—*e.g.*, with straggling *Rubus fruticosus agg.*, and such herbaceous species as *Nepeta glechoma*, *Lychnis dioica*, *Circaea lutetiana*, *Viola* spp. Independently of the suitability of this low scrub or herbaceous layer as judged by comparison of its structure with that of open scrub or grassland, it is nevertheless uniformly unsuitable for the grasshoppers considered here, for the shade determining this structure also cuts out the direct insolation necessary for normal activities of grasshoppers. The position of incompletely closed woodland or scrub is not so simply defined, however; this naturally grades into the types of low open scrub already mentioned as generally favourable to grasshoppers, but it becomes less favourable in its opposite gradation towards the undergrowth of closed scrub and woodland. In general this decreasing suitability is associated with increasing height and density of the herbaceous and scrub components. Thus in woods on heavy damp soils even extensive clearings commonly show vegetation too tall and thick for any grasshoppers at all to occur—*e.g.*, clearings in oakwood on clay with such frequent species as *Deschampsia caespitosa*, *Calamagrostis epigeios*, *Epilobium hirsutum*, *Spiraea ulmaria*, *Carex* spp., *Valeriana officinalis*, *Cnicus palustris*, *Angelica sylvestris*, *Rumex acetosa*. The drier parts of this community are less unfavourable, however, and in woodland on poorer and drier soils the tendency towards thinner and less uniform structure may provide good conditions for *G. rufus*, or *C. parallelus*, in the more extensive clearings and even for the more geophilous *C. bicolor* or *M. maculatus* in the poorest type of scrub clearings. For instance, enclaves on the chalk scrub may vary from irregular but moderately dense vegetation of the order 20–60 cm. high, with *G. rufus* and *C. parallelus* in concentration of 0·1–0·3 per square metre, to very poor *Cornus sanguinea* scrub with 50–80 per cent. cover, under rabbit pressure, supporting local populations of *C. bicolor* and *M. maculatus* up to 3–6 per square metre, and with *C. parallelus*, *S. lineatus* and *G. rufus* more thinly and generally distributed. Size and frequency of such enclaves in relation to the total amount of woodland are important factors in determining their grasshopper population, in addition to structure of vegetation. Small and infrequent enclaves rarely have a high population, independently of the scrub structure, no doubt because of the difficulty in initial colonisation together with the transience of the suitable vegetation in small enclaves, in which development toward full woodland cover is usually rapid. Further, none of the grasshopper species considered here occurs early enough in the year to take advantage of the spring vegetation of the more open woods, notably open canopy oakwood, which might well provide a suitable habitat were it not that by the end of May dense shade develops, and undergrowth is succeeded by the thin summer growth of closed woodland.

Degree of exposure to the sun has also important effects on open communities of grassland or scrub; again it is difficult to disentangle the effect of sun or shade on the suitability of structure of vegetation from the immediate dependence of grasshoppers on exposure to direct sunlight, but it is worth while to consider shortly these effects on suitability of structure. The general effect of the amount of exposure

to direct sunlight, especially when reinforced by exposure to wind, dryness of soil, and slope, is to decrease density, uniformity and height of the herbaceous layer. In comparatively level types of neutral grassland, including most of the agricultural grassland to be found in South England, this factor is unimportant in comparison with the others also determining structure, but on poorer acid or basic soil, with steeper slopes, the difference between a north and a south aspect may produce a very significant difference in vegetation structure. On the chalk, for instance, south-facing steep slopes support poor and thin Festucetum ovinae, while equally steep north-facing ones commonly bear dense cover of the order 5–20 cm. high, with such species as *Bromus erectus*, *Festuca rubra*, *Avena pratensis* replacing *Festuca ovina* and *Carex flacca*, and great development of the moss layer with *Hylocomium* spp., *Bracythecium purum*, *Hypnum molluscum*, *Camptothecium lutescens*, etc. In extreme cases, at White Horse Hill, Berkshire, where the chalk scarp faces north for instance, even denser and taller cover may be found, with *Bromus erectus* and *Brachypodium pinnatum* as the main grasses, even *Deschampsia caespitosa* locally, *Poterium sanguisorba* forming a dense layer between the interstices of the grass tufts, and such moisture and shade-loving mosses as *Hypnum cuspidatum* locally, and *Fissidens taxifolia* and *Mnicum undulatum* under the general herbaceous layer; such structure is certainly prohibitively dense for grasshoppers, except very locally, and the unfavourable effect is reinforced by exposure to wind and absence of sun. In less degree, however, this effect may be enough to contribute largely to the difference between dense 5–20 cm. Brometum erectum with much *Poterium sanguinsorba*, occurring on a 5–10° north slope (as is not uncommon locally on the dip-slope of the chalk in Surrey, for instance), which supports *C. parallelus* and *O. viridulus* at the levels of 0·1–0·3 per square metre, and thinner more varied *Festuca rubra-ovina–Bromus erectus* grassland on a corresponding south slope (on the crest of the North Downs, for instance) with a richer population of *C. parallelus*, *S. lineatus*, *G. rufus*, and to less degree *C. bicolor* and *O. viridulus*, at a general level of 1–3 per square metre. Rabbit pressure may modify this effect of shade structure in an interesting way. A severely rabbit-infested steep north slope of the Chiltern scarp (at Shirburn Hill, Oxfordshire) showed development of mosses to a higher degree even than that mentioned above, with *Bracythecium purum*, *Camptothecium lutescens*, *Hypnum cupressiforme*, *H. molluscum* and *H. schrebei*, *Hylocomium triquetrum*, *H. squarrosum* and *H. splendens*, *Ceratodon purpureus*, *Bryum*, etc., forming a very thick soft fibrous turf mixed with *Festuca ovina* (grazed very short, down to moss level) and *Helianthemum vulgare*; the turf was discontinuous, with intervening bare stony patches with abundant growth of *Iberis amara* in season, and though the texture of the turf was far too soft and fibrous to favour egg deposition, the general shortness of the turf (< 5 cm.) and the irregular cover (*ca.* 80 per cent.) gave conditions favourable enough for sporádic occurrence of *M. maculatus* (0·1–0·3 per square metre), in spite of the steep north-facing slope. On the adjacent west-facing slopes or level ground, with equal rabbit infestation, much thinner and less

regular Festucetum ovinae showed local concentrations of 1–3 per square metre. The bad effects of a north slope on vegetation structure were modified enough by the impoverishing effect of rabbit grazing to produce a structure tolerable for *M. maculatus* in spite of exposure to wind and low incidence of sunlight. Another interesting case of unequal distribution of sunlight on a much more local scale is that of mounds of the ant *Acanthomyops flavus*, often common in poor scrub and grassland. On the south and west sides and the top of these, vegetation is generally thin, especially when, as is very common, rabbits are frequenting them ; on the north and east sides it may often be much denser and taller. Thus in chalk grassland or scrub the shaded sides may bear dense cover, 5–10 cm. high, of *Lotus corniculatus*, *Helianthemum vulgare*, *Origanum vulgare*, *Brachypodium sylvaticum*, *Festuca rubra*, with *Bracythecium purum* and *Hypnum cuspidatum* abundant, while the sides exposed to the sun bear thin *Festuca ovina* and irregular prostrate mats of *Thymus serpyllum*, with much bare soil. The more sociable species of grasshoppers, especially *C. parallelus*, *C. bicolor*, *M. maculatus* and *C. albomarginatus*, congregate very strikingly on the thin vegetation and bare soil of these sun-warmed sides of the mounds, leaving the denser sheltered sides and to a less extent the general level of the vegetation much less densely populated, if at all. However, it should not be supposed that these effects of sun and shade on structure of vegetation are a more important factor than the direct needs of grasshoppers for sun and warmth ; the two factors are usually coexistent and adjuvant, but in a few cases—*e.g.*, in one or two records of north-facing 80–50 per cent. irregular *Rubus fruticosus* scrub with very low grasshopper populations—there was no obvious unsuitability of structure, and sunlight was obviously a directly determining factor.

The varying role of mosses has been mentioned from time to time in this discussion of the herbaceous layer, especially in connection with the factor of shade. In some cases, as in very short turfs, and heaths or chalk grassland with very irregular cover, especially under rabbit pressure, their structural role is indistinguishable from that of phanerogams of the herbaceous layer, but in most examples of closer and richer grassland and scrub they make a definite contribution towards the general density, on a level below that of the herbaceous layer. The maximum development of this third or moss layer occurs in more or less shaded habitats, whether they be the north and east-facing slopes just described, or marginal scrub and grassland associated with woodland. The richest types of grassland under good illumination show such mosses as *Fissidens taxifolia* (especially in Brometum erecti), *Mnium undulatum* and *M. affine*, and thin poor forms of *Bracythecium rutabulum*, low down among the bases of the grass tufts ; such species emphasise the unsuitability of the damp shaded ground for grasshoppers rather than contribute to the unsuitability of the vegetation as a whole. Thinner types of grassland show a higher development of *Bracythecium rutabulum* and *B. purum* among the tufts, but in well-illuminated habitats this is irregular and not of great importance for the total density, especially in summer, though in winter it becomes propor-

tionally more prominent. Shaded grassland of the moderately vigorous type very often shows a dense interstitial growth of mosses between the grasses, making it certain from structure as well as from general climatic conditions that the conditions are very unsuitable for grasshoppers; enclaves of fairly thin and short grassland in woodland, or stretches on the edges of woodland, especially by the sides of paths, not uncommonly look superficially moderately suitable for grasshoppers, yet there may not even be erratic adult individuals to be found. In these cases the degree of infiltration of the herbaceous layer by mosses is a ready indication of the general unsuitability of ground conditions and the local absence of such a dense moss growth is commonly correlated with at least sporadic appearance of adult grasshoppers. In general, prominence of mosses in all but the poorest grassland is a good indicator of unsuitability; this is particularly so in the case of *Hypnum cuspidatum*. Moderately damp but thin neutral grassland with a moderate growth of *Bracythecium rutabulum* and perhaps quite favourable to *C. parallelus* or *C. albomarginatus* (densities of the order 1-3 per square metre) occasionally shows locally slightly damper patches in which general structure of vegetation is not grossly changed, but the dampness is sufficient to encourage replacement of *B. rutabulum* by a denser growth of *H. cuspidatum* among the grass, and grasshoppers are here much less frequent (*e.g.*, low-lying meadows in Oxfordshire and Berkshire by the Thames, show this well). *H. cuspidatum* is in some cases a good indicator of waterlogging or actual flooding of the soil in the winter, and the effect of this on survival of eggs through the winter must be considered.

To summarise, the features of vegetation found to be most significant for grasshoppers are :—

(1) Little or no interference with the access of direct sunlight to the herbaceous layer and the soil.

(2) Height and density of texture of the herbaceous and scrub layers determine the amount of penetration of light and warmth into the vegetation and down to the soil, while in impeding air movement and direct falling of rain into the deeper layers they provide shelter against adverse climatic conditions.

(3) Factors most important in controlling height and density are :—

(*a*) Size and growth-form of the dominant species—optimal development of the latter in the better types of grassland dealt with here is almost always unfavourable, and modifying factors are needed to produce favourable conditions.

(*b*) Poorness of soil, especially with extremes of acid-base balance, is the most important single factor modifying vegetation structure towards suitability for grasshoppers : it tends to reduce, and to produce irregularities of, height and density of the herbaceous layer, and eventually to produce discontinuity, with incomplete vegetation cover and exposure of bare earth ; all these tendencies are towards more favourable conditions for grasshoppers.

(*c*) Nature and amount of grazing and treading of the vegetation tend to produce a short herbaceous layer of dense texture which is not usually a favourable type of habitat, but in more excessive degree they may

produce irregularities of height and density, and conditions under excessive grazing may become very favourable.

(*d*) Amount of exposure to direct sunlight, already listed, has striking effects on the structure of grassland, as well as modifying suitability of this and other habitats in a more direct way; height, density, and especially development of a thick moss layer, are all increased by shading, which is thus unfavourable both in modifying the total access of light and warmth to the vegetation, and the distribution of the light and warmth through the detailed structure of the latter.

(4) Operation of these factors in most cases tends to irregularity of structure, with diversification of local microclimatic conditions, of which several examples have been noticed above. Scrub probably provides the most striking examples of such localization, as the scrub layer must be discontinuous and irregular to provide suitable conditions for grasshoppers.

(5) It has been pointed out that the aspects of vegetation considered here are selected as related to environmental conditions for grasshoppers, independent of their degree of correspondence with botanical classification of such vegetation. Though this is the primary emphasis, the two lines of approach are not sharply divided, and it will have been noticed that more than once it has been valuable to consider the instability of the plant community in relation to scrub changes, as well as its local structure, in order to account for features of grasshopper distribution.

After an analysis of this sort the limited value of the gross classification used in Table 1 can be appreciated. A striking example is provided by the category 100 per cent. $< 5$ cms. In Table I this category contains 16 records, of which 14 showed low densities, under 1 per square metre. These included 6 cases of closely cattle-grazed neutral grassland; 3 cases of closely trodden paths; and 5 cases of moderately heavy rabbit pressure on poor soil, 3 of them dense close-grazed mixtures of the typical herbaceous species of chalk scrub with very little grass, and two *Festuca ovina* or *Festuca-Agrostis* grassland, also fairly close and dense. The remaining 2 records, one with a density of 1–3 per square metre, the other $> 10$ per square metre, were also Festucetum ovinae under rabbit grazing, but both of them less dense, whether due to poorer or greater rabbit pressure not being very obvious. The record of $> 10$ per square metre is not easy to account for even so; it is the highest uniform adult density found (*ca.* 45 per cent. each of *C. parallelus* and *G. rufus*, 10 per cent. *S. lineatus*), yet analysis of its various features does not suggest a significant difference of conditions from the similar habitat with 1–3 per square metre. The very important factor of which the incidence is least well shown in the tables is that of localization of important environmental conditions, and more specific discussion of this point will be resumed later.

### *Vegetation as Food.*

Acrididae in general may be considered essentially phytophagous; cannibalism in populations confined under experimental conditions is definitely exceptional. In the fairly extensive series of observations in which grasshoppers were watched feeding under natural conditions,

there was no indication of any predatory attitude towards small animals, such as the Psyllids which were occasionally found in grassy habitats in great numbers, or of any tendency to eat dead animal matter of any sort.

Theoretical consideration suggests that the characteristics of the vegetation as food which might be important for grasshoppers are :—

(1) Mechanical properties which might make it difficult to approach, or chew, or to digest.

(2) Palatability, determined by both mechanical and chemical factors, and perhaps involving psychological factors of inherited or acquired habit.

(3) Chemical properties which might determine total or specific nutritive value.

A thorough investigation of the problems mentioned would require an amount of care and labour such as has not yet been spent on the nutrition of any group of insects, but nevertheless there are numerous recorded observations on food preferences as observed under more or less natural conditions. Hodge (1933) described the effects of diets composed of various species of plants on the development of *Melanoplus differentialis;* Carothers (1923) and Criddle (1933) made observations on food plants of various N. American ACRIDIDAE ; Rubtzov (1932) did the same for Siberian species, while Isely (1938) made a thorough experimental investigation of food preferences of some forty species of Texas ACRIDIDAE. In general these observations show that most species show some degree of preference for particular food plants, usually grasses, but that these preferences are by no means rigid, and are much conditioned by the total range of plants available. Isely, however, found that several species, notably of the subfamily CYRTACANTHACRINAE (not represented in the British fauna), had quite rigid preferences, so that a particular food plant might be a limiting factor for such a species ; he also found that ACRIDINAE (to which subfamily all British species belong) had a general preference for grasses as against other herbs.

It has not been possible in the present work to investigate systematically this question of food, but such incidental observations as have been made confirm the conclusion that ACRIDINAE show a general preference for grasses, and are not confined to specific food plants.

### *Field Observations on Feeding.*

Whenever in the course of field observations an individual was seen to make a good meal of a particular plant (as distinct from nibbling at the edge of a leaf and passing on) a record was made of the species of grasshopper and plant, and these records are presented in Table 2. This table shows a great preponderance of records for grasses ; it is not possible to derive many detailed conclusions, however, without taking into account the relative abundance and availability of the various plant species under the conditions in which the records were made. For instance, more records were obtained for *Festuca rubra* and *Festuca ovina* than for *Lolium perenne* or other species of neutral grassland, largely because a high proportion of the watching was done in chalk grassland and scrub. Also each species of grasshopper may contribute

TABLE 2.

Numbers of recorded field observations when a grasshopper species was seen feeding on a species of plant.

| | *S. lineatus* | *O. viridulus* | *M. maculatus* | *C. bicolor* | *C. parallelus* | *Ch. albomarginatus* | *G. rufus* | Total |
|---|---|---|---|---|---|---|---|---|
| GRASSES | | | | | | | | |
| *Festuca rubra* / *Festuca ovina* ... | 4 | 4 | 5 | 9 | 29 | — | 14 | 65 |
| *Lolium perenne* | — | 2 | — | 12 | 22 | 4 | 1 | 41 |
| *Dactylus glomeratus* | 2 | 2 | — | 3 | 7 | 2 | — | 16 |
| *Arrhenatherum elatior* ... | — | — | — | — | 3 | — | — | 3 |
| *Bromus erectus* ... | 1 | — | — | — | 2 | — | 5 | 8 |
| *Agrostis tenuis* ... | 2 | 3 | 9 | 16 | 11 | — | 4 | 45 |
| *Agrostis alba* / *Agrostis canina* | — | 2 | — | — | 3 | 1 | — | 6 |
| *Cynosurus cristatus* | — | — | — | 3 | 4 | 2 | — | 9 |
| *Anthoxanthum odoratum* ... | — | — | — | 1 | — | — | — | 1 |
| *Deschampsia flexuosa* ... | — | — | 3 | 1 | — | — | — | 4 |
| *Deschampsia caespitosa* ... | — | — | — | — | 2 | — | — | 2 |
| *Brachypodium pinnatum* ... | — | — | — | — | 1 | — | 1 | 2 |
| *Carex flacca* ... | 2 | — | — | — | 4 | — | 2 | 8 |
| *Briza media* ... | 1 | — | — | — | — | — | 1 | 2 |
| *Poa* spp. ... | — | 1 | — | 2 | 6 | 3 | — | 12 |
| Total for grasses | 12 | 14 | 17 | 47 | 94 | 12 | 28 | 224 |
| HERBS | | | | | | | | |
| *Poterium sanguisorba* ... | 3 | 1 | — | — | 6 | — | 7 | 17 |
| *Lotus corniculatus* | 4 | — | — | 3 | 8 | — | 4 | 19 |
| *Trifolium* spp. ... | — | — | — | 9 | 7 | 2 | — | 18 |
| *Asperula cynanchica* ... | 1 | — | — | — | — | — | 2 | 3 |
| *Viola hirta* ... | — | — | — | 1 | — | — | — | 1 |
| *Galium* spp. ... | — | 1 | — | 3 | 1 | — | — | 5 |
| *Achillea millefoliam* ... | — | — | — | 2 | — | — | — | 2 |
| *Fragaria vesca* ... | — | — | 1 | — | — | — | — | 1 |
| *Thesium humifusum* ... | — | — | — | — | — | — | 1 | 1 |
| *Hypericum perforatum* ... | — | — | — | — | 1 | — | 1 | 2 |
| *Rumex acetosella* | — | — | — | — | 5 | 1 | — | 6 |
| *Lathyrus pratensis* ... | — | 1 | — | — | — | — | — | 1 |
| *Taraxacum officinale* ... | — | — | — | 2 | 1 | — | — | 3 |
| *Medicago lupulina* | 2 | — | — | — | 1 | — | 1 | 4 |
| *Origanum vulgare* | — | — | — | — | — | — | 1 | 1 |
| *Plantago media* ... | — | 1 | — | 1 | 3 | — | — | 5 |
| Total for herbs ... | 10 | 4 | 1 | 21 | 33 | 3 | 17 | 89 |

proportionally more to the total records of one plant than to those of another, not necessarily because of variations in palatability, but also because of variations of abundance of these plants in the various habitats of the grasshopper. Thus *G. rufus* and *S. lineatus* appear to feed more frequently on *Festuca* spp. than on the *Agrostis* spp., for they are typically species of chalk grassland and scrub, while *M. maculatus* and *C. bicolor*, distributed over a greater variety of soils, especially in heathy habitats, have relatively more *Agrostis* records ; yet though the numbers of records are rather small and difficult to interpret in the light of relative abundance of different grasshoppers, there seems no reason to suppose that, *e.g.*, in Festucetum ovinae the *Festuca* is any more preferred by *G. rufus* than by *C. bicolor*. The table gives an idea of the plants commonly eaten under natural conditions when the supply of food is apparently not a limiting factor, but its figures cannot be interpreted in terms of relative palatability of plants or specific preferences of different grasshoppers.

Further, a few detailed conclusions may be drawn from Table 2. For instance, *Bromus erectus* is a much commoner grass in the chalk habitats observed than its total number of records relative to *Festuca* spp. would lead one to suppose ; comparative unpalatability of this grass may contribute to the unsuitability of dense uniform Brometum erecti for grasshoppers ; the same may apply, though the grass is less common, to *Brachypodium pinnatum*. Among herbs, only *Poterium sanguisorba*, *Lotus corniculatus* and *Trifolium* spp. are recorded more than casually ; they were commonly abundantly available, but often no more so than several other species of which there are no, or few, records—such common species as *Achillea millefolia*, *Hypocharis radicata*, *Plantago* spp., or the mosses *Bracythecium rutabulum*, *B. purum* and *Camptothecium lutescens*. That there must be marked differences of palatability among members of a plant community of comparable abundance is evident from the general preponderance of records for grasses, and the above points about the most abundant herbs ; it is also confirmed by consideration of a chalk grassland community in which more records were made than for any other single community (Table 3). Incidentally, it should be noted that no records were made of mosses being eaten.

TABLE 3.

Feeding records for a chalk grassland community. (Colley Hill, Surrey.)

1. Composition of Vegetation.

| | |
|---|---|
| *Bromus erectus.* | *Inula conyza.* |
| *Festuca ovina.* | *Viola hirta.* |
| *Carex flacca.* | *Clinopodium vulgare.* |
| *Cirsium acaule.* | *Hypericum perforatum.* |
| *Hieracium pilosella* | *Campanula rotundifolia.* |
| *Helianthemum vulgare.* | *Thesium humifusum.* |
| *Lotus corniculatus.* | *Gentiana amarella.* |
| *Poterium sanguisorba.* | *Fragaria vesca.* |
| *Asperula cynanchica.* | *Potentilla reptans.* |
| *Galium verum.* | *Camptothecium lutescens.* |
| *Thrincia hirta.* | *Fissidens taxifolia.* |
| *Origanum vulgare.* | *Hylocomium splendens.* |
| *Linum catharticum.* | *Hypnum molluscum.* |

2. Concentrations of Adult Grasshoppers.

*Gomphocerus rufus.*
*Chorthippus parallelus.*
*Stenobothrus lineatus.*
*Chorthippus bicolor.*

3. Feeding Records.

| | *G. rufus* | *C. parallelus* | *C. bicolor* | *S. lineatus* | *Total* |
|---|---|---|---|---|---|
| *Festuca ovina* ... | 5 | 4 | — | 2 | 11 |
| *Carex flacca* ... ... | 1 | 1 | — | — | 2 |
| *Poterium sanguisorba* ... | 1 | 2 | — | 1 | 4 |
| *Lotus corniculatus* ... | 1 | — | 1 | 1 | 3 |
| *Bromus erectus* ... | — | 1 | — | — | 1 |
| *Asperula cyanchica* ... | 1 | — | — | — | 1 |
| *Galium verum* ... ... | 1 | — | — | — | 1 |

*Food Preference of Captive Grasshoppers.*

In order to get some idea of how far these findings were related to the total supply and the variety of plant food available, experiments were made in which adults of *C. parallelus*, *C. bicolor*, *G. rufus*, *S. lineatus* and *M. maculatus* were confined in their natural habitats or on a garden lawn, under jam-pots. About five individuals were confined under each two-pound jam-pot at a time, and the composition of the vegetation enclosed was noted at the start of each experiment, and daily or every other day thereafter; altogether 45 experiments of this sort were made. It seemed clear that the grasshoppers were not adversely affected by the abnormally humid and warm conditions provided; the mortality observed was 8 out of 210 individuals, each experiment lasting on the average five days, while fresh individuals were taken for each confinement. Indeed this method was also used for breeding of nymphs with fair success; from second instar to adult overall mortality was 11 per cent. (out of a total of 132), while from first instar to adult it was 24 per cent. (out of a total of 85), even though drying and hardening of the cuticle at each moult was very slow and incomplete. Thus though conditions were obviously not optimum (reproductive activity of these bred individuals was very poor compared with that of wild adults caught and similarly confined), high humidity may not always be as strikingly unfavourable as *e.g.*, Sansome and La Cour (1930) suggest.

Because of the small number of these experiments, and the limited time available for them, it has not been possible to record the detailed order of rapidity and thoroughness with which the various plants were eaten, but three rough groups may be recognised :—

I. Readily eaten during the first one to two days of a five-day experiment :—
*Festuca ovina*, *F. rubra*, *Agrostis alba*, *A. tenuis*, *Poa annua*, *Carex flacca*, *Avena pratensis*, *Dactylus glomeratus*, *Lolium perenne*, *Lotus corniculatus*, *Medicago lupulina*, *Poterium sanguisorba*, *Trifolium repens*.

II. Eaten as the supply of group I ran out :—
*Achillea millefolia*, *Bromus erectus*, *Galium vernum*, *Asperula cynanchica* (moderately readily eaten); and *Viola hirta*, *Bellis perennis*, *Fragaria vesca*, *Origanum vulgare*, *Potentilla reptans*, *Plantago media* (usually only partly eaten).

III. Almost, or completely, untouched in five days :
*Cirsium acaule*, *Helianthemum vulgare*, *Thymus serpyllum*, *Hieracium pilosella*, *Clinopodium vulgare*, *Cerastium vulgatum* and all the mosses observed.

One or two other species might also have been included — for instance *Taraxacum officinale* and *Linum catharticum* in the first group — but they were not observed often enough. These results are by no means intended to be exhaustive lists, even for the limited habitats observed ; the main conclusion to be drawn from them is that they show a rough gradation of palatability among a few common plants ; the degree to which some species are positively unpalatable is better shown than in the observations on quite undisturbed feeding, though even here some eating of the third group might have been noticed if the confinement had been longer.

It is noteworthy that the species of the first group include many of those most often recorded in the watching observations, and that again they are mainly grasses. It is difficult to pick out characters likely to be responsible for the unpalatability of the second and third groups ; mechanical properties (*Thymus serpyllum*, *Helianthemum vulgare*) and prostrate, especially rosette, habit (*Bellis perennis*, *Cirsium acaule*, *Hieracium pilosella*), are possibly important. Watching unconfined individuals suggests that their tendency to steady a leaf between the two fore-legs, with its flat surface in the sagittal plane of the body, so that the edge of the leaf is chewed in the course of a characteristic downward sweeping movement of the head, may be a factor in their preference for the thin and usually flat and tender leaves of species of the first group. In confined conditions, however, as the vegetation is selectively eaten down, this habit rapidly becomes less obvious.

Incidentally, the fact that five grasshoppers in such a confined space took at least three to four days to eat all the palatable vegetation available is some indication of the extent to which even the uncommon examples of 3·6 or higher densities per square metre fall short of those necessary to have a serious effect on the vegetation. Another point worth comment is that the chalk grassland commonly showed proportionally much more unpalatable residue after five days than did the neutral grassland, in which commonly the only residue was *Braeythecium rutabulum*, *Cerastium vulgatum*, and partly eaten *Bellis perennis* or *Plantago media*.

To summarise the general conclusions of this discussion on food :

1. Present observations agree with previous work in showing that Acridinae are phytophagous, with a limited degree of preference for particular plants especially most grasses. There was little evidence that in the habitats observed the nature or total amount of edible vegetation present was an important factor in determining occupation of those habitats. Such preferences as were observed seemed very much of relative rather than absolute nature.

2. No cases were observed in which concentration of grasshoppers and consequent intensity of feeding appeared to modify strikingly the amount or structure of the vegetation ; neither were any instances

observed of more specific deleterious activity. It does not seem likely that grasshoppers are ever abundant enough to have significant economic effects over the area observed.

## Soil Properties.

Properties of the soil may have an importance for grasshoppers apart from their influence on vegetation. The most important of these are the thermal properties of bare exposed soil, which determine its suitability for basking and the associated stridulatory activity of geophilous species, and the attributes such as mechanical consistency and seasonal variation in water content which determine suitability for deposition and survival of egg-pods.

Thermal properties which influence the rate of uptake or loss of heat by different soils have been little investigated; the water content of the soil is important, but other factors such as closeness of structure and content of organic matter are probably also significant. Grasshoppers have been noticed to congregate most on dry well-drained soil sloping towards the south, but comparatively fewer cases were observed of wet soil being exposed than of the drier and generally poorer types; the range of habitats was also not wide enough to permit careful investigation of the relative attractiveness of peaty as against predominantly mineral soils. It can be said, however, that exposed areas of dry readily warmed soil interposed among vegetation are very regularly the sites of congregation of grasshoppers in locally high concentrations in sunny weather. One special case is of interest: Fruhstorfer (1921) mentions that late in the year highest numbers of various species were to be found in the sun on fallen leaves, usually beech-leaves. In my observations, there was noticed several times, in chalk grassland adjacent to beechwood, or in thin scrubby enclaves in beechwood, a tendency for *C. bicolor*, *M. maculatus*, and *G. rufus* especially to congregate and bask in the sun on small collections and drifts of last year's dead beech leaves (also one late example, 15.ix.44, of high concentrations of *G. rufus* on a thick layer of dry dead pine-needles). Wisps of hay usually left on a mown field, or piles of dried vegetable matter left after the tending of roadsides, are often attractive to grasshoppers, and probably largely because of their favourable thermal properties, *C. parallelus* and *C. albomarginatus* were often found to take advantage of them.

The problem of suitability of soil for deposition and survival of egg-pods is a very important one. Unfortunately, populations of grasshoppers met with are generally too low, and the labour of estimating frequency of egg-pods so as to draw significant conclusions about relative suitability of different soil properties too great, to make any detailed observations possible in England. Given the factors determining such suitability, however, it will be possible to draw some conclusions about the importance that deposition and survival of eggs have in occupation of various habitats. These factors are variations in mechanical properties of the soil, in its water content, in its exposure to adverse environmental influences such as extremes of temperature, and in its disturbance during the year.

The consistency of the soil determines the readiness with which it is pierced by the ovipositor, and with which it can be searched by predators —*e.g.*, by birds' beaks. The first is a possible limiting factor for occupation of some of the unsuitable habitats observed, such as very stony ground with low percentage cover on chalk, or grassland subjected to repeated treading; excessive hardness, whether discontinuous or more uniform, must tend to limit the distance to which the ovipositor can penetrate, and the more shallowly an egg-pod lies, the less chance it has of surviving extreme weather conditions, or disturbance by active agents. Probably coarse-textured but moderately firm soils in well-drained positions over sand or chalk are optimum. Not a great number of habitats on clay soil was observed, but it seemed probable that poor drainage with consequent higher water content is more important than mechanical consistency *per se* for lesser suitability of clay; poor drainage leads particularly to wider seasonal variations in water content, which will prejudice survival of eggs over the winter. The heavier soils in any case tend also to be less favourable, in supporting richer vegetation, with less access to the soil. It is difficult to be sure how far seasonal waterlogging is an important limiting factor; for instance, alluvial meadows by the Thames, subjected to grazing and annual mowing for hay, usually showed poor and irregular grasshopper populations, yet occasional cases with a similar degree of waterlogging during the winter did show higher densities, and the sites of egg-laying or of early nymph concentrations were not necessarily in the drier and better drained parts of these exceptional meadows.

One aspect of density of vegetation at least which should be favourable to grasshoppers is the shelter it provides not only to adults but also to eggs in protecting them from extreme fluctuations of temperature. Here, as elsewhere, uniform density is likely on balance to be disadvantageous, but localised shelter should be significantly advantageous, the more so in more exposed habitats, and where egg-pods are less deeply buried. Seasonal changes in development of vegetation may affect the amount of soil exposed, and so modify this insulating effect of vegetation on soil; in chalk grassland, for instance, in winter the dying-back of such species as *Cirsium acaule*, *Poterium sanguisorba*, *Lotus corniculatus*, and increase of development of the characteristic mosses, often makes the pattern of exposure of soil quite different from that in summer; also in mixed bracken and grass heath habitats the bracken litter in winter may locally increase the insulating power of other vegetation.

It is probable that soil conditions for optimum survival of eggs may be so precise as only to be locally distributed in otherwise generally fairly suitable habitats: some of the often striking localisation of nymphs to be next described may be related to localised egg deposition as well as to exacting environmental requirements of the nymphs themselves. In general the present discussion suggests that soil properties may often contribute directly to the suitability of grasshopper habitats, but not many examples have been found in which such properties are limiting, to the exclusion of significant features of vegetation.

### Nymph Distribution.

Consideration of the greater sensitivity of nymphs to adverse environmental conditions (*cf.* Hamilton, 1936), their possible exposure to a greater range of these, their limited motility, and their lesser strength, make it likely that they should show more strict localisation than adults to favourable microclimatic conditions. Several observed examples show this localisation very strikingly. Each habitat was examined closely comparatively early in the season to determine the features of soil and vegetation of the areas in which nymphs were mainly concentrated, and estimations of their mean concentrations in these areas and in the rest of the habitat; later in the season estimations of mean concentrations of adults in these areas, and in the rest of the habitat were again made.

For scrub habitats observed in this way the characters of areas particularly favoured by nymphs were largely those also favourable to adults, but within narrower limits of variation. Short, thin, usually grassy vegetation, with generally some exposure of bare soil here and there, but not on a large scale, and often made more favourable by shelter of surrounding vegetation, were the important characters, observed in examples of scrub both from the chalk and from sandy heaths. For instance, a typical case of chalk scrub consisted of fairly tall and dense-growing species which formed a rich irregular growth up to 0.5-1 m. high together with the straggling *Rubus fruticosus* and *Rosa* spp. Plants of a thin herbaceous growth of the order of 2–5 cm. high and 100-80 per cent. cover occurred locally among this richer growth. Counts made at the beginning of August showed that *C. parallelus* and *C. bicolor* were present mainly as adults, but with a few nymphs, while *G. rufus* was present almost entirely as nymphs. In the thin short vegetation the mean density of nymphs of all species was 5 per square metre and of adults 2 per square metre; elsewhere the nymph density was nil, and the adults 1 per square metre. Four weeks afterwards, the corresponding values were for the short vegetation, nymphs 0.4 per square metre, adults 3 per square metre; elsewhere nymphs still nil, adults 1 per square metre. Here the greater degree of localisation of nymphs is quite obvious.

Several types of grassland habitats were also investigated in this way —untended irregular grassland, road and track-sides subject to occasional mowing, and meadows used for hay and grazing. Each showed the same limitation of nymphs to relatively short and thin vegetation, though generally to a less striking degree than the scrub example just given. One example should suffice out of the eight cases observed—one of irregular heathy grassland remarkable for supporting a pure population of *O. viridulus* of quite high concentration. The general composition of its vegetation was :

*Festuca rubra.*
*Agrostis alba stolonifera.*
*Potentilla erecta.*
*Dactylus glomeratus.*
*Achillea millefolia.*
*Galium saxatile.*
*Holcus lanatus.*
*Hypochaeris radicata.*
*Deschampsia flexuosa.*
*Arrhenatherum elatius.*
*Leontodon hirtus.*
*Anthoxanthum odoratum.*
*Hieracium umbellatum.*
*Poa pratensis subcaerulea.*
*Plantago lanceolata.*
*Stellaria graminea.*
*Agrostis tenuis.*
*Festuca ovina.*
*F. commutata.*

Here the general vegetation was fairly dense, irregular, with 100 per cent. cover and height up to 20–60 cm. and composed of the first sixteen species in this list ; locally quite frequent, however, was a short turf of fair density and 100–80 per cent. cover, composed notably of the last three species in the list, and also some of the smaller ones of the rest of the list—*e.g.*, *Galium saxatile*, *Potentilla erecta*. At the end of June there was a concentration of 10 nymphs and 0.5 adults of *O. viridulus* per square metre in these short grass areas, and 1 nymph and 0.3 adults per square metre in the rest of the association. In the first week of August there were 2 adults per square metre in the short grass areas, and 1 per square metre in the rest ; the numbers of nymphs observed were not enough for significant estimations to be made.

The expectation that nymphs would show more restricted habitat preferences is thus verified. It is consequently probable that requirements of nymphs rather than of adults determine in practice the suitability for grasshoppers of the various features of structure and composition of vegetation discussed here. The limited results on nymphs indicate that the same main factors are involved in suitability of habitat as for adults, and that the difference is one of stringency of demands for similar suitable features. Examination of habitats for the degree of localisation of features which provides conditions suitable for nymphs as well as for adults becomes an important aspect of their appraisal ; conditions uniformly favourable for nymphs are likely to be provided by optimum habitats, but the majority of habitats in this country are less uniformly good, and whether they contain locally suitable areas will determine whether they are breeding habitats, or are suited only to casual or erratic visits.

## The General Question of Localisation.

In every part of this discussion the importance of local diversification of vegetation structure, and hence of microclimatic conditions, has been emphasised in relation to each factor considered. It has been concluded that not only may a local occurrence of favourable conditions, in a habitat generally unfavourable, be enough to allow higher permanent density of a species in a given habitat than would superficially be suspected, but also that local diversity of structure may provide for the varying requirements of grasshoppers in different phases of diurnal activity and at different stages in the life-history. Now that the individual factors significant for the satisfaction of these requirements have been discussed, it may be profitable to examine the localisation observed in a few habitats of typically varied local structure and composition, and consider it in terms of all the factors likely to be operating.

The first example is an irregularly dry corner of an upland bog in Monmouthshire. Its general vegetation composition was :—

| | | |
|---|---|---|
| *Agrostis tenuis.* | *Ulex nana.* | *Narthecium ossifragum.* |
| *A. canina.* | *Potentilla erecta.* | *Juncus effusus.* |
| *Deschampsia flexuosa.* | *Polygala vulgaris.* | *Eriophorum augustifolium.* |
| *Erica cinerea.* | *Sphagnum* spp. | *Orchis maculata.* |
| *E. tetralix.* | *Carex inflata.* | *Bracythecium purum.* |
| *Vaccinium myrtillum.* | *C. acutiformis.* | *Polystichum commune.* |
| *Betula pubescens.* | *Scirpus caespitosus.* | |

The first group of species occurred on relatively raised areas of dry and well-drained peaty soil, the second in the intervening waterlogged areas ; no account has been taken here of the more specialised vegetation at the sides of little streams cutting deeply through the peat to join up these waterlogged parts. There is thus a primary distinction between parts of the association with soil seasonally or permanently dry, and parts permanently waterlogged, and it is very probable that deposition and survival of eggs will have been confined to the drier soil. Beyond this however, each type of vegetation shows some structural differentiation relevant to distribution of grasshoppers ; the drier parts were partly covered with an irregular shrubby growth of *Erica* spp., *Vaccinium myrtillum*, *Betula pubescens*, *Ulex nana*, with some grasses, but there were also areas with much dark peaty soil exposed, and a short thin growth of *Agrostis tenuis*, *Deschampsia flexuosa*, *Potentilla erecta*, *Polygala vulgaris* ; the wet areas bore either a thick growth of *Sphagnum* spp., *Polytrichum commune*, *Narthecium ossifragum* and *Eriophorum angustifolium*, or a taller more grasslike growth with dense basal tufts rising above the water level, of *Carex* spp., *Scirpus caespitosus*, *Juncus effusus*. In mid-June, nymphs of *C. bicolor*, *C. parallelus* and *M. maculatus* were very abundant (mean 8 per square metre) on the dry thin patches, and no individuals were noticed elsewhere. In August, adults of *C. bicolor* and *M. maculatus* were found in a density of 2 per square metre on the dry thin patches, with adults of *C. parallelus* occasional 0.3 per square metre ; in the dry shrubby growth adults of all three species were found casually, while adult *C. parallelus* reached a mean density of 0.2 per square metre in the *Scirpus- Carex- Juncus* areas. Here it is probable that localisation of soil water was mainly important in determining distribution and survival of eggs, while the further localisation of vegetation structure was significant for habitat selection by nymphs as a whole, and by adults according to specific preference ; it is probable also that the denser shrubby growth round the dry thin patches provided shelter at times for both nymphs and adults.

The second example shows more clearly the role of localisation in providing shelter as well as favourable conditions for activity. It is a case of short irregular chalk scrub, and the shrubs present were so scanty that the localisation to be described is within the structure of the herbaceous layer only. The vegetation consisted of :—

| *Cornus sanguinea.* | | *Betula pubescens.* |
|---|---|---|
| *Poterium sanguisorba.* | *Hieracium pilosella.* | *Carlina vulgaris.* |
| *Cirsium acuale.* | *Viola hirta.* | *Campanula glomerata.* |
| *Lotus corniculatus.* | *Clinopodium vulgare.* | *Blackstonia perfoliata.* |
| *Asperula cyanchica.* | *Hypericum perforatum.* | *Centaurium umbellatum.* |
| *Thrincia hirta.* | *Thymus serpyllum.* | *Pieris hieracoides.* |
| *Festuca ovina.* | *Brachypodium sylvaticum.* | *Inula conyza.* |
| *Carex flacca.* | *Linum catharticum.* | *Scabiosa columbaria.* |
| *Origanum vulgare.* | *Euphrasia nemoralis.* | *Cladonia* spp. |
| *Bracythecium purum.* | | *Camptothecium lutescens.* |
| *B. rutabulum.* | | |

This formed a thin continuous mat about 2–5 cm. high, subject to moderately heavy rabbit grazing, on a gentle slope (*ca.* 5°) facing towards

north-west. The grazing was remarkably even, so that even *Brachypodium sylvaticum* conformed with the general 5 cm. height limit, though around the infrequent scattered shrubs it might rise to a 20 cm. with *Poterium*, *Origanum*, *Clinopodium*, etc. Hence apart from these occasional sheltering patches of more vigorous growth the general distribution of external factors determining density and growth form of the herbaceous layer was very uniform, so evidence of localisation within this herbaceous layer is interesting in showing the importance of differences of growth-form in different species of plant under similar environmental conditions in the same association. The general structure of the herbaceous layer was very thin and scrappy; even *Poterium sanguisorba* was too overgrazed to provide any density to the very short irregular growth, so that most species were reduced to the same prostrate condition as the rosette-forming *Cirsium acaule*, *Hieracium pilosella*, *Thrincia hirta*, which have already been noticed as unsuitable in producing density of ground cover with no depth to it. In spite of this there was in late August a general density of *S. lineatus*, *G. rufus* and *C. parallelus* of 0.3 per square metre on a hot sunny day, yet in early morning the concentration to be observed by very careful search through the general vegetation was a good deal less, in fact at the sporadic level of $< 0.1$ per square metre. There were quite abundantly scattered among the general vegetation, however, areas with fairly strong dense growth of *Festuca ovina* up to 3–4 inches high, with *Viola hirta*, *Clinopodium vulgare* and some increased development of *Poterium sanguisorba*; in these areas densities up to 1 or 2 per square metre were observed in the early morning—clearly better shelter against cool night conditions was provided by this denser and leafier growth with slight depth to it. The taller growth round the shrubs also showed this shelter effect, and also permitted higher concentrations in the sun on the south side of the shrub than were noted in the general vegetation.

The last example is of scrubby grass heath on sand, and illustrates most strikingly the effect of tall shrubs with dense vegetation at their base in sheltering the shorter vegetation around. The general composition of the vegetation was :—

| *Rubus fruticosus* (agg.) | | *Ulex europaeus.* |
|---|---|---|
| *Festuca ovina* and *rubra.* | *Hieracium pilosella.* | *Teucrium scorodonia.* |
| *Agrostis tenuis.* | *Hypochoeris radicata.* | *Ornithopus perpusillus.* |
| *Deschampsia flexuosa.* | *Crepis capillare.* | *Polygala vulgaris.* |
| *Holcus lanatus.* | *Hieracium umbellatum.* | *Achillea millefolia.* |
| *Carex* sp. | *Galium saxatile.* | *Trifolium repens.* |
| *Cynosurus cristatus.* | *Spergularia arvensis.* | *Hypericum humifusum.* |
| *Dactylus glomeratus.* | *S. rubra.* | *Filago germanica.* |
| *Bracythecium purum.* | *Rumex acetosella.* | *Ceratodon pupureus.* |
| *B. rutabulum.* | *Polytrichum juniperium.* | *Bryum* sp. |
| | *Hypnum cupressiforme.* | *Mnium rostratum.* |
| | *Dicranum scoparium.* | |

The fairly bulky *Rubus* and *Ulex* bushes or the order 1 m. high were surrounded at their bases by a dense and irregular growth of taller grasses and herbs, notably *Festuca rubra*, *Holcus lanatus*, *Agrostis tenuis* *Teucrium scorodonia*, about 10–30 cm. high; there were also patches

of fairly dense more uniform vegetation (about 10–20 cm. high, 100 per cent. cover) associated with only scattered straggling *Rubus*, with similar species; finally the general vegetation consisted of a short thin 2–5 cm. growth with 80–100 per cent. cover composed of most of the species of the list, except *Holcus lanatus*, *Dactylus glomeratus*, *Teucrium scorodonia* and the shrubs. In early July, nymphs of *C. parallelus*, *C. bicolor* and *M. maculatus* were locally very abundant among the short vegetation, with a mean density of 4 per square metre over the whole area, rising locally to 10–12 per square metre often in the shelter of *Ulex* and *Rubus* bushes, but also quite often in areas not strikingly distinguished in structural composition of vegetation or other environmental features from the general characters of the short vegetation. Adults of *C. bicolor* and *C. parallelus* were infrequent and occurred sporadically throughout the short vegetation, but *M. maculatus* adults were more abundant, and showed similar localisation to that of the nymphs occurring in the same local aggregations associated with shrub shelter or in general vegetation (mean density in these places 3 per square metre), and also abundantly in the sun on a small south facing sandy bank with 30–40 per cent. cover of thin *Agrostis tenuis* and *Deschampsia flexuosa*, patches of *Polytrichum juniperum*, and straggling *Spergula arvensis* (mean density 4–5 per square metre; nymphs were not frequent here, perhaps because of the much scantier cover). In mid-August nymphs had become infrequent, but adults of all three species were abundant over the general vegetation in mean density of 2 per square metre; in locally thin areas with reduced cover *C. bicolor* and *M. maculatus* were more abundant in the heat of the day, especially on the sandy bank (mean density 4–5 per square metre), but *C. parallelus* was no more abundant here than in the more grassy parts. In the shelter of shrubs facing south, all three together reached densities of 4–5 per square metre, and *C. parallelus* was here relatively more abundant, and extended more into the thicker taller vegetation round the shrubs, while it was the only species to reach an appreciable density (1 per square metre) in the denser *Holcus*, *Teucrium*, *Festuca rubra* patches. Points illustrated by this example are localisation in relation to density of cover, and also to shelter by scrub growth, and relative preferences of nymphs as against adults, and of different species of adults, for conditions of soil exposure and vegetation structure. This habitat also shows some tendency for aggregations of nymphs or adults (most strikingly *M. maculatus*) within areas of the general vegetation of apparently uniform structure; the significance of such localisation of occurrence independent of variation of local environmental conditions is of some general interest, and will be discussed below.

This small group of examples could be expanded almost indefinitely for about 80 per cent. of the habitats observed showed localisation of important features of the environment, whether of soil conditions, variable incidence of biotic factors modifying vegetation, or the casual variations of structure and specific composition of vegetation within an association exposed to roughly uniform external agencies; commonly, as in present examples, several significant features of this sort occur simultaneously in the same habitat.

## Problems of Motility and Sociability.

In the last section the possibility that gregariousness or limited motility may be also factors in local irregularity of distribution was mentioned. Results relevant to this question of normal range of movement were obtained by watching the behaviour of undisturbed or marked individuals, and by determining rate of spread of larger numbers of marked individuals from the area in which they were initially marked and liberated ; observations were also made on power and range of movement after disturbance.

More extensive observations were made on adults than on nymphs, and so adults will be considered first ; the more limited results for nymphs will then be described and compared with the fuller picture obtained for adults.

### *Movement on Disturbance.*

Maximum range of a single jump, assisted or not by wings, depends in adults on a number of factors : morphological characters such as degree of wing development, development of hind femora, bulk of the body, which account for most sexual and interspecific variability ; factors determing metabolic activity and alertness, such as temperature and humidity ; and such external factors as nature of the site of taking off, and strength of wind and its direction in relation to the initial direction of leaping. When one adds to these the more subtle sources of variation like the nature of the disturbing agent, it becomes clear that to obtain a reliable index of maximum range of movement from the mean of large numbers of random leaps, even under conditions fixed as nearly optimal as possible, would be a very laborious task, and for practical purposes it is sufficient to observe the rough order of size of maximum leaps noticed in the absence of serious distortion by wind or slope. During routine observations and other investigations, in good weather conditions, records were made therefore of large leaps which were particularly noticed in adults and also in some nymphal stages of each species. It was found that the possible range of a single leap assisted or not by wings was of the order of 3 metres in female *C. parallelus*, and up to the order of 6–8 metres in males of most of the larger species and in female *C. bicolor*.

The question of range of movement on disturbance requires further analysis, however ; there are also involved the number of times an initial jump is repeated, and the nature of onset of fatigue ; also the question whether the direction of such progression continues to be related to the site of the disturbance, and whether the nature of the disturbing agent has any effect on size, repetition or direction of the leaps. The collector with any experience of the British species is likely to have a good idea of the answer to these questions in so far as they concern repeated following up of a specimen with a view to catching it. In weather favourable to grasshopper activity, a grasshopper which is followed up may leap six to eight times in a few seconds without noticeable diminution in length of leap ; in other words, a persistent predator may stimulate several emergency leaps in succession, but as this supposed predator is

following up each leap fairly closely there is no necessary uniformity of direction shown by successive leaps. Repeated and methodical observation, however, indicates that this is only a special case of operation of a number of factors. Both height of disturbing agent, and its distance from the grasshopper, are important factors in determining type of response to disturbance: thus only in the case of disturbances of the order of height of a man will repeated leaping be commonly seen if the first leap is of more than about two metres, and only if the hypothetical collector moves towards the site of alighting is a leap likely to be repeated more than once, or, if repeated, likely to continue to be obviously away from the observer. With smaller predators, the chance of repeated leaps with a stationary disturbance, and the distance between disturbance and grasshopper necessary for further stimulation, became correspondingly much less. Some time was spent in watching, from cover and with a field-glass, the technique of blackbirds and starlings in catching grasshoppers, and the behaviour of the grasshoppers, at fairly close range. It seemed that a bird of this size only disturbed grasshoppers from a distance of about 30 cm. around and in front of it; that leaps were brisk but did not generally approach the size produced by human stimulus under similar conditions; and that repeated leaps were very uncommon. A bigger bird, the kestrel, could not be observed so closely, but the observation suggested a much wider zone of disturbance around it, associated no doubt with its habit of hunting grasshoppers by hovering at a height of 2–3 metres and doing a miniature "stoop" for each captive, as well as with the bigger size. Another point occasionally observed with human disturbance is that sudden disturbance with a poor first jump and poor conditions for landing and further take-off may cause an apparent panic with repeated unco-ordinated kicks, which make the grasshopper very conspicuous and presumably very easy for a bird or similar predator to capture. If, however, the grasshopper seems to fall casually on to better take-off conditions, such as are normally automatically sought for during the period of readjustment after landing and preparatory to another leap, a successful leap may occur, and even be followed by others, indicating that the panic only results in temporary inco-ordination, and does not give rise to fatigue.

Leaping, repeated if necessary, is of course not the only response to disturbance, but it is a common and regular one among the species considered here. Burrowing into densely matted vegetation, such as well-grown *Helianthemum vulgare* or *Thymus serpyllum*, was frequently observed at the end of a leap, as also was the related habit, frequent in tall grass vegetation, of alighting on or striking a vertical stem and sliding down it to burrow and hide among the denser growth below. From the point of view of survival value some such habit as burrowing or becoming completely immobile after the initial leap seems much more useful than repeated leaping; blackbirds and starlings most commonly caught grasshoppers immediately after their landing from a leap, and in a few cases it was possible to see the slight movements associated with recovery of balance before the grasshopper was taken. Probably if conditions happened to be right for immediate immobility

or for burrowing into the vegetation the predator would find detection less easy—the birds observed often were unable to see or to take anything after eagerly following up a first leap. Of course, this behaviour of birds is well recognised in connection with OEDIPODINAE, whose flash colours in flight and immobility on landing, with obliterative resting patterns, seem undoubtedly of survival value. At all events the difference of behaviour according to size of disturbing agent is interesting: Professor G. D. Hale Carpenter (*in verbis*) pointed out that the same phenomenon is probably responsible for the habit of some African grasshopper-eating birds of associating with cattle, in that the cattle in moving disturb grasshoppers far more extensively than the birds themselves could do.

### *Normal Behaviour and Movement Without Disturbance.*

Watching normal behaviour in the field without disturbance soon shows that leaping of the type just described is very uncommon, and is of the order of centimetres rather than metres. The characteristic type of activity of adults of all species involves deliberate walking or climbing movements, with interruptions for feeding or stridulation; only when progress by walking becomes difficult or involves going back again from the position reached is leaping resorted to, and the leap is then short, usually single, and often seems more directed towards a particular site of landing than do leaps after disturbance. The direction of progression is very commonly, particularly in high densities of grasshoppers, towards a stridulating male or a nearby female, leading to concerted bursts of stridulation among males, or almost interminable advances and withdrawals and circumambulations of males and females. It is remarkable how often this mutual approach and drawing back of males and females has been watched for long periods without its having been seen to lead up to copulation; it has been reported in the past as a courtship activity, though only by inference. In fact, in present experience grasshoppers were rarely observed *in copula*—records kept for the last four years with the object of finding how indiscriminate is pairing between individuals of different colour varieties have only so far reached a total of 45 instances. It might be supposed that pairing in natural conditions is of short duration or generally under shelter of vegetation, but at any rate there seems little evidence that the very common stimulation of activity of males and females by each other's presence is necessarily courtship behaviour. Related to this is the gathering of several males around a single female; the female may pay more or less attention, and seems often quite indifferent, but the males walk around and stridulate each against the other with great energy; stridulation of males is also commonly observed without a female, especially on patches of bare ground, such as the sunny sides of *Acanthomyops flavus* mounds; in general males indulge in sociable activities of this sort to a much greater extent than do females. Description of observations on normal activity could be carried further, in greater detail; undisturbed behaviour of grasshoppers is a most interesting subject for observation and is sometimes of considerable complexity, but the importance of no disturbance should be stressed, for lack of due care in approaching and

watching may induce a state of alertness, short of actual alarm and leaping away, which at least temporarily inhibits normal patterns of activity; it is well worth while approaching slowly, keeping close to the ground, and using local cover where practicable, to avoid this possible disturbance. Enough has been said here, however, to illustrate how sociability enters into normal behaviour.

The next point of particular interest concerns the range of these normal limited movements—*e.g.*, whether the concentration occurs in relation to particular places in the environment, and whether particular individuals continue to be associated together for long periods or only transiently during peregrinations over perhaps quite a wide area. To test these questions individuals from areas of congregation were netted under the standard net-covered metre quadrant frame used for density estimations; each was marked with a distinguishing mark in oil paint on the pronotum, and they were then liberated within the area of capture. A difficulty arose here which was important in all the experimental observations on normal undisturbed movement: a movement casually induced by disturbance while making the observations was likely to be of a much greater order of size than the movements it was hoped to investigate. All that could be done about this was to be continually careful to avoid disturbance where possible—for instance, in avoiding marking and especially liberation and recapture in weather conditions very favourable to general activity—and to bear in mind the possibility of occasional large casual distortions in individual results, so as to keep the operation of them as random as possible, inevitably reducing preciseness but not necessarily producing distortion of the pooled results. It was possible to cut down wide scattering satisfactorily by postponing liberation until weather was reasonably cool and dull; further observations were by watching, in which disturbance was not important. Such marking was done for one colony of *C. bicolor* and one of *G. rufus* and *S. lineatus*; three cases of *Acanthomyops flavus* mounds with a mixed population of *C. parallelus* and *C. bicolor* were also investigated. For the two colonies no striking difference was noticed between the behaviour of the three species; out of a total of eight separate markings, each of the population of a selected square metre with good aggregation, there were marked 44 males and 21 females of all species, and of these 23 males and 10 females were subsequently seen inside the appropriate square metre on at least one later occasion, and 13 males and 4 females on more than one occasion. Each square metre was observed for half-an-hour on the first and second days after marking. The discrepancy between those marked and those subsequently seen must be partly due to a wider dispersal of marked individuals, but 12 males and 3 females were also seen immediately around the test square metre, though not actually inside it. Thus, about three-quarters of those marked were subsequently seen in or near the test areas: during the periods of observation a few individuals were noticed to move into or out of these areas, but in general movement during observation was irregular and random, and few marked individuals pursued the same course for long. Activities during observation were of the general nature already des-

cribed : on the whole females wandered more freely than males, with movements less obviously related to other individuals around them, and without any obvious preference for a particular spot in the area, or a very limited range : males were occasionally seen to wander freely like females, but they spent much more time in sociable activities, such as stridulating, within a very limited area of movement, which commonly centred in a particular patch of bare earth or sun-warmed vegetation. These males commonly remained in relatively stationary groups composed of the same individuals during the whole period of watching. Particularly interesting is the observation that in four cases two males were still in association in roughly the same spot on successive days : that is, 8 out of the 11 males observed within the test areas on successive days showed sociable behaviour on the same spot and with the same individual.

Conclusions suggested by these observations are that normal range of movement during undisturbed activity for two successive days is of the order of size of 1 metre, rather than of the maximum leaping powers recorded : and that a noticeable degree of social activity, particularly of males, takes place within this limited range, and involves some degree of constancy of association with particular individuals and with a particular place. The observations on populations of *Acanthomyops* mounds were planned similarly, and involved half-hour periods of watching on two successive days after marking : the results were similar, and in particular one case of repeated association on successive days of two males, and one case of three males, were observed. Unfortunately, all these observations could not be continued longer than two days, and there was also no opportunity to test the fidelity of association with a particular place by liberation of individuals at a distance from the place of capture and marking. Some experiments on marking and liberation in a rather larger area, and observation of distribution of these marked individuals up to ten days afterwards, but without protracted watching, were however, devised and carried out.

The general plan of these last experiments was to select linear habitats of the order of 1–2 metres wide, such as roadside or trackside grassy verges, or banks of similar restricted width, so that if the population of a particular segment of this were marked and liberated in sites, their diffusion to each side along the axis of the strip could be observed, while excessive loss of marked individuals in other directions was limited by the narrow extent of the habitat. Finding suitable habitats of this sort, with fairly uniformly populated strips of the order of 40 metres long, was not easy, but observations were much easier than if diffusion in all directions had been tested ; altogether six suitable colonies were found, three of *C. bicolor* and three of *C. parallelus*. Each experiment was done by taking 35 metres of the selected strip and dividing it into seven parts, each 5 metres long. All adult grasshoppers in the middle 5-metre strip were captured, marked (all with the same mark, not with the distinguishing marks for each individual that were used in the watching experiments), and liberated *in situ*, with precautions to avoid excessive alarm and scattering. Subsequently, on the second, fourth,

sixth and tenth days after liberation, the whole 35 metres were thoroughly searched (by hand and with a small hand net, but without systematic capture), and the distribution of marked individuals in the seven 5-metre strips was recorded. To minimise scattering during these observations they were made towards evening, when activity was falling off. In spite of care during searching, disturbance and scattering were not wholly avoided, but in order that this should not adventitiously disturb the distribution in one particular direction, search was made in opposite directions along the 35 metres on successive days of observation. Had it been possible to avoid disturbance, the distribution would probably have been even more localised, with little or no spread to outlying strips.

The results of these experiments are represented diagramatically in Fig. 1, which shows the pooled observations of three experiments

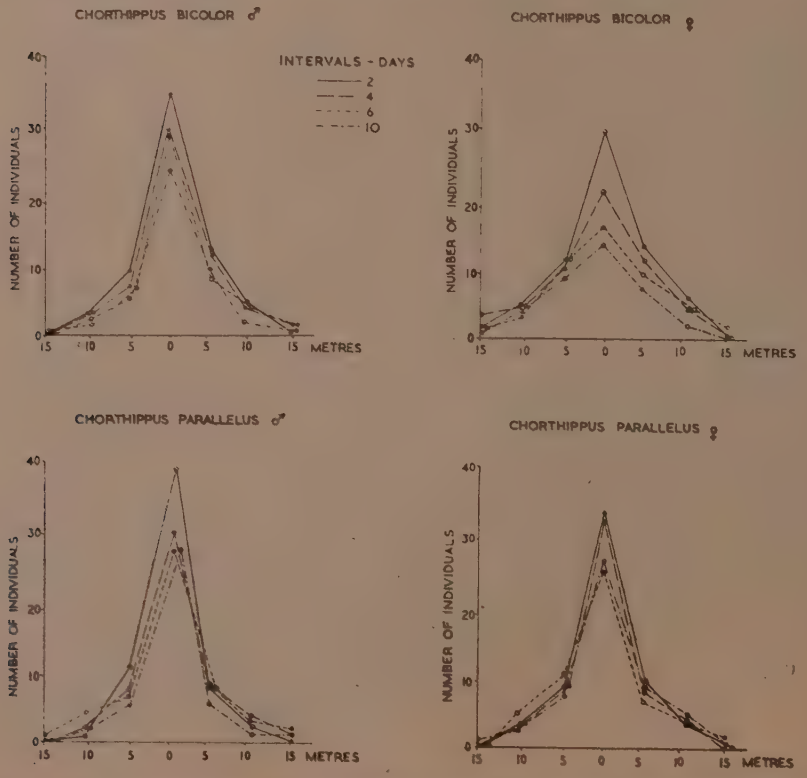


FIG. 1.—Dispersion of adults of *Chorthippus bicolor* and *Ch. parallelus* marked and liberated within an initial strip 5 metres long, after intervals of 2, 4, 6, and 10 days. The middle of the initial strip marked as 0; figures to the right and left of it give distance of the middle of each 5 m. strip from 0. Each point on the curve represents the sum of determinations from three separate experiments.

for *C. bicolor*, male and female, and *C. parallelus*, male and female, respectively. The general approximation of the distributions to normal frequency distributions is what is to be expected if the process studied is one of lateral diffusion. The interesting points are the degree of increasing lateral spread with successive observations, and the greater spread shown by females of *C. bicolor* than by the others. It is tempting to relate their greater spread to wider range of normal activity and wandering, and the lesser spread of the males of both species to sociability and limited range of normal activity. The *C. parallelus* female results suggest that degree of wing-development—*i.e.*, range of maximum leaps—nevertheless plays a part in the wider diffusion of *C. bicolor* females, for the apterous *C. parallelus* females have not spread so widely. With present size of the experiments the differences of distribution are suggested rather than fully demonstrated, but the method seems promising, and the tentative conclusions fit in with the arguments and results already presented.

Summarising the main points about normal range of movement: Normal undisturbed activity involves little or no leaping, and its progress is to be measured in centimetres rather than metres. It involves a good deal of social activity, especially on the part of males, and over short periods at least there may be continued association between particular individuals and with particular places. Gross distribution and diffusion, observed over periods of ten days, involve spread both by normal activities and by disturbance, with big leaps; it is difficult, and indeed not wholly desirable, to try to separate completely the effects of these two factors, and at all events the results on gross distribution show a marked preponderance of records from the area of initial capture suggesting that normal activity is mainly within a range of dimensions of 5 metres or less over periods up to ten days, but that the sociability and attachment to a particularly locality which this may involve can be overcome by casual external disturbance, with consequent wider diffusion.

General implications of these results are relevant both to technical questions and to the general theoretical argument of this work.

To take the theoretical considerations first. The limitation of normal undisturbed range, apparently determined largely by sociability, in spite of the ability to move rapidly over much greater distances when necessary, suggests that gregarious behaviour is probably an important reinforcing factor in maintaining concentration in local microclimatically suitable parts of the environment. In fact, it seems improbable that this local concentration is simply a transient phenomenon in the lives of individuals which spend their time wandering widely over a given habitat, having at any moment a greater concentration in favourable than in unfavourable localities, but not being individually limited over a period of time to the same restricted area. It seems more likely that individuals are to some degree associated with particular limited areas, so that they may congregate repeatedly in the same place, and that wider diffusion is due mainly to casual disturbance from this normal limited activity. The much greater range provided by power of leaping

on disturbance gives a basis for understanding wide diffusion of adults over areas unsuitable for occurrence of nymphs (examples of Vestal's "erratic" occupation of habitats). On the other hand, sociable activity is a check on this tendency to wide diffusion, and accounts for a degree of concentration and localisation, which might not at first be suspected in animals potentially so mobile. The wide range of possible diffusion provides in its turn a check on the tendency of sociability to produce rigid localisation with possible isolation of local variations, and it is probable that the relation of variation to local isolation is a very fruitful problem with Acrididae. However, casual diffusion by disturbance is likely to be a powerful enough mixing factor to eliminate isolation of small groups. The greater the discontinuities of environmental structure, *e.g.*, of vegetation, the more efficient will isolation be, even against the wider powers of diffusion ; one or two cases have been noticed of gradual development of scrub vegetation over a period of four years, such that the taller scrub elements now form a much more serious barrier to free mixing of the initially fairly uniformly distributed population than was present at first.

Technical implications of the observations relate to two experimental methods used (the routine estimations of density, and the recapture frequency) and also to the general question of sampling grasshopper populations by any method. The success of any recapture frequency method depends on efficient mixing of marked individuals with the rest of the population, so where mobility is limited in relation to the size of the area under investigation marked individuals should be liberated as nearly as possible at random over the habitat, and not in relatively few places ; in the observations described here each individual was liberated at its place of capture and marking, care being taken to traverse the whole habitat fairly. As for the routine method of estimating density, it was desirable that the net-covered metre quadrant should be dropped so as to imprison and not to startle away the grasshoppers in the area, and that examination of larger areas should be done with minimal disturbance ; as already described, precautions were taken to minimise effects of disturbance, and in particular estimations were as far as possible not made in conditions optimal for grasshopper activity. In fact, any method of determining total abundance, and especially any one which involves sampling by sweep net or hand picking, must take account of these phenomena of detailed localisation of grasshoppers in a habitat, and also of the factors of motility and disturbance which influence this distribution ; the reproducibility of any method of sampling is particularly dependent on variations of activity of the insects and on the degree of care taken by the observer in dealing fairly with local variations in abundance.

## Discussion.

In the preceding sections a number of generalisations have been made concerning the relations of grasshoppers to their environment, based on observations made in various localities in southern England. It is very necessary to examine the limitations of these generalisations before they can be considered of any value.

In the first place, all the observations were made in a single uniform area, and to that extent their applicability to other geographical areas may be limited, at least as regards maters of detail. Further, the fauna of ACRIDINAE of this area is not large, for the climatic conditions are not optimal for them, the members of the fauna all being relatively vigorous non-exacting species of wide geographical distribution, such as are commonly described by workers in the continent of Europe as "trivial" or "ubiquitous." They are also correspondingly less abundant here than in the more favourable parts of their range, and their demands on favourable local structure of the environment may be more exacting than in regions of more generally favourable climatic conditions.

Second, most of the conclusions arrived at, with the interpretations put on them, are based on relatively indirect and uncontrolled inference from observations; few of the conclusions have been experimentally tested. It is desirable to follow up deductions about environmental conditions in relation to structure of vegetation by direct determinations of ranges of temperature and humidity associated with the various features of structure; it would then be of great interest to make experimental determinations of microclimatic requirements of the various developmental stages of the species considered here, as *e.g.*, Hamilton (1936) has done for three African locust species, and relate these to the microclimatic conditions actually observed in the local distribution of these species in the field. The present work can therefore only be considered as a first step towards investigation of the ecology of British ACRIDINAE in relation to microclimates. Further extension is desirable, too, for elucidation of the problem propounded by Bei Bienko (1930), of the different optima of the same species in different geographical zones; investigation of the microclimatic conditions associated with local vegetation structure in the different geographical zones would test and develop Bei Bienko's hypothesis that local conditions in vegetation of similar general structure vary with broad geographical differences of climate.

Some general conclusions emerge, however, from the limited observations described here. On starting this work I was impressed by the often striking localisation of occurrence of grasshoppers, which might be explained by any of the three factors—local environmental differentiation, limited ability to spread and colonise adjacent habitats, and some positive social tendency determining aggregation rather than diffuse distribution. It is now clear that local differentiation of habitats is a factor of some complexity, and may account for a large part of the localisation. Occasionally, however, local aggregations were found independently of any obvious variation of environmental conditions; this may of course have been due to the crude methods of observation used here, and it may be that if direct temperature and humidity records were taken even greater microclimatic differentiation might be found than is here inferred from variation of topographical or botanical features of the environment. The possibility remains open, nevertheless, that sociability and limited tendency to spread may be important in determining local distribution; the fact that this area is towards the limits of the geo-

graphical range of the species considered may account for limited powers of spread and failure to occupy all possible suitable habitats over the area. Sociability, on the other hand, is a factor which from present observation and from the work of others is found to be more important as total abundance rises, and so either at low or high level of abundance some factor other than environmental differentiation may be expected to play some part.

Another question relevant to interpretation of results is that of fluctuations of numbers of individuals in a given habitat. It was mentioned earlier that routine single estimations of grasshopper density in a habitat, though quantitatively expressed, were only given within fairly wide limits of accuracy, and that this was due not only to the errors possible in making the estimation, but also to possible errors introduced by fluctuations of abundance either during the season or from year to year.

Though the inferential method used here is crude and needs confirmation by other methods, the results do emphasise the need for care and attention to detail in describing topography, soil or vegetation of grasshopper habitats ; it is necessary to know not only the plants present, but their relative proportions and their particular growth-forms in the habitat considered, and to observe the variations in these features in different parts of the habitat, and this also of course applies to questions of soil, slope or shelter.

Another result of the limited favourability of conditions in south England is that grasshoppers can rarely or ever be abundant enough to be an important biotic factor in modification of vegetation ; at least no clear example of such an effect was noticed here, and populations of nymphs and adults were never found great enough to make it probable. This agrees with the general experience that they have no economic importance in this country. They are, on the other hand, significantly influenced by the effects of common methods of agriculture on soil and vegetation ; disturbance of soil by ploughing, or various types of grazing, are important factors determining their occurrence, and the most favourable habitats observed here have been agriculturally derelict or useless land. Abundance of grasshoppers on agricultural land in this country, as in others, is an index of poor soil or of poor farming, though here it does not carry the penalties of mass outbreaks that it may do elsewhere.

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